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BIOCHEMISTRY AND MOLECULAR BIOLOGY

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Preface

Nearly twenty years ago one of us (S. P. D., soon joined by G. H. S.), began a distillation of the elements of biochemistry into an alphabetical arrangement. The task was formidable and eventually other editors were recruited, an editorial board was established, and now the work is offered as the *Oxford Dictionary of Biochemistry and Molecular Biology*. It is hoped that the dictionary will serve the needs of the research biochemist or molecular biologist, as well as teachers of the subject and their students. In addition, it should prove of value to practitioners of other fields of study or work seeking the meaning of a biochemical term.

An important function of a dictionary is to provide guidance on current usage in the field within its scope. The original 12-volume *Oxford English Dictionary* was compiled from about five million slips of paper bearing sentences or phrases extracted by some thousands of 'readers' from classical works of literature and those of the best contemporary authors. It was thus firmly based on good usage. In scientific subjects, specialist terminology is often codified in sets of recommendations regarding nomenclature, meaning, abbreviations, symbols, and so on. These have been agreed by international commissions (e.g. those of The International Union of Pure and Applied Chemistry and The International Union of Biochemistry and Molecular Biology) as a means of preserving order and facilitating communication between scientists. We have striven to conform as far as possible to the relevant international recommendations, but in some cases, where usage so frequently diverges from a recommendation that adherence to it would seriously detract from ease of use of the dictionary, we have kept to the principle that the dictionary should reflect usage (see the definitions of *lexicographer*). This does not extend, of course, to cases where usage, however widespread, contradicts sound scientific principles. The internationally agreed recommendation is always also listed. The various compilations of these recommendations that have been drawn upon are listed in Appendix B, together with a number of other sources of information on nomenclature.

Biochemistry is the discipline that embraces the study of the structure and function of life-forms at the molecular level. Molecular biology is a closely related discipline that originates in the study of DNA and its metabolism, and now embraces all those investigations that exploit the technology that has resulted from this work. Both disciplines aim to explain the behaviour of life-forms in molecular terms, and are so closely interrelated that separation is barely possible. It is inevitable that the content of this dictionary is to a degree arbitrary, but it is hoped that all important aspects of these subjects have received consideration. The compilers have attempted to offer a broad coverage of terms encountered in the literature of biochemistry and molecular biology by including an appreciable number from cognate sciences. Although the compilation is designed primarily to serve readers of contemporary material, the needs of those who turn to older literature have also been borne in mind. Some of the entries thus have a historical flavour, some obsolete terms are included (e.g. zymase), and in some cases a historical approach has been used as the best means of presenting an explanation of a term, as for example in the case of the entry for *gene*. The value of a scientific dictionary is enhanced by inclusion of contextual information as well as mere explanations of meaning or terminology. This dictionary will be found to have some of the attributes of an encyclopedia, although the extent to which it veers in this direction has varied with the whim of its compilers. It is our hope that in a single volume the reader has easy access to basic definitions as well as a generous helping of other information.

In the present-day world, we are assailed by floods of 'information'. It has been suggested that the average weekday edition of a newspaper of record (e.g. *The New York Times*) provides more information than Shakespeare and his contemporaries would have acquired in a lifetime. With the availability of much information through the Internet, it may be asked whether a dictionary in paper form is actually necessary. In answer, we note that the Internet can be slow, and is not readily accessible in some parts of the world; the databases may be inadequate, and although usually very up-to-date, the high cost of their maintenance restricts them to specialized knowledge in a limited number of fields. Moreover, books have a

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quality of their own, which is enabling them to maintain their popularity. It appears that the increasing use of the Internet is actually paralleled by the rate of publication of printed dictionaries; in an information-hungry age, there cannot be too many sources of good-quality information.

We are deeply indebted to the Leverhulme Trust for the award of an emeritus fellowship to one of us (A. D. S.), to University College London, which has provided us with friends and expert colleagues, and to Dr O. Theodor Benfey, Dr Mary Ellen Bowden, and Professor Arnold Thackray, The Beckman Center for History of Chemistry, Chemical Heritage Foundation, Philadelphia, and Dr John Edsall, Harvard University for assistance with biographical data.

Particular thanks are due to Dr H. B. F. Dixon for much advice on nomenclature and related matters. Help on questions of nomenclature from Dr G. P. Moss and Dr A. D. McNaught is also acknowledged. We are grateful to Dr D. H. Jenkinson for his help with the recommendations of the International Committee on Nomenclature in Pharmacology. We are also grateful for the valuable advice of Professor K. W. Taylor and Dr J. L. Crammer, on clinical topics, and Professor M. C. W. Evans, on plant biochemistry, and to Dr Margaret McKenzie, for reading the proofs.

During the earlier stages of the project, Mrs S. Gove gave much valuable assistance and Miss A. Straker was most helpful in suggesting terms for inclusion. We also wish to thank all those other friends and colleagues, in addition to those separately listed, who have unstintingly given us help and advice.

We are pleased to acknowledge the collaboration and material support given to us by Oxford University Press. We also acknowledge the very friendly cooperation of Market House Books, especially the patience and good humour of Dr John Daintith through all the complications of the production. The copy editors, Robert Hine and Jane Cavell, made a number of helpful suggestions.

The compilers offer no apology for their failure to include many deserving terms in the dictionary, but would be pleased to have their attention drawn to errors and to receive suggestions for additional entries in any future edition.

Correspondence concerning the dictionary is best addressed to the Managing Editor, *Oxford Dictionary of Biochemistry and Molecular Biology*, c/o Oxford University Press, Great Clarendon Street, Oxford OX2 6DP

January 1997

A. D. Smith
S. P. Datta
G. H. Smith
P. N. Campbell
R. Bentley
H. A. McKenzie

This whole book is but a draught—nay, but the draught of a draught. Oh, Time, Strength, Cash, and Patience.

Herman Melville (1851) *Moby Dick, or The Whale* (ed. T. Tanner, 1988, p. 147, Oxford University Press).

Preface to the revised edition

It must be inevitable with any work of this nature that a number of imperfections and errors occur. So the opportunity provided by the need to reprint this dictionary has been taken to effect some improvements within the limitation imposed by retention of the original pagination. As well as the correction of a variety of minor misprints and other minor defects, over four hundred entries been either revised or completely rewritten, and fifty or so new entries have been provided, some to remedy deficiencies and others to provide additional terms that have become of topical interest. To help make way for the new ones, about half as many original entries have been deleted. In addition, Appendices B, C, and D have been updated, and Appendix B has been expanded and provided with all the relevant Internet addresses available at the time of writing.

Valuable comments on the original edition by a number of readers are gratefully acknowledged, and thanks are again due to Dr. H. B. F. Dixon for advice on aspects of nomenclature as well as to Oxford University Press and Market House Books for their much appreciated cooperation.

September 1999 A. D. S.

Note on proprietary status

This dictionary includes some words which are, or are asserted to be, proprietary names or trade marks. Their inclusion does not imply that they have acquired for legal purposes a non-proprietary or general significance, nor is any other judgement implied concerning their legal status. In cases where the editor has some evidence that a word is used as a proprietary name or trade mark this is indicated by the designation *proprietary name*, but no judgement concerning the legal status of such words is made or implied thereby.

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Guide to the Dictionary

1. Alphabetical order

1.1 Main order of headwords

Alphabetical order is determined on a letter-by-letter basis, not word by word; spaces are disregarded:

acid
acid anhydride
acid–base balance
acid–base catalysis
acid dissociation constant
acid dye
acidemia

1.2 Nonalphabetic characters

Numbers, hyphens, primes, and subscript/superscript text are ignored for the purpose of indexing; an example is the following sequence of entries:

FSH-RH
F1 sphere
F′ strain
F-type pentose phosphate pathway
ftz

1.3 Locants and modifiers

In chemical names, any locants and other hyphenated modifiers such as *cis*-, *trans*-, *p*-, and alphabetic Greek characters are not used to determine primary alphabetical order; hence the following entries all appear under the letter A:

***N*-acetylgalactosamine**
***p*-aminobenzoic acid**
***γ*-aminobutyrate shunt**
6-aminohexanoic acid

However, the unhyphenated letters 'c' in 'cDNA' and 'd' in 'dCTP', for example, are treated as integral parts of the word and *are* used to determine alphabetical order.

1.4 Secondary order involving locants

When such modifiers constitute the only difference between two headwords, they determine the alphabetical order of the entries:

benzodiazepine	**encephalitis**
***o*-benzoquinone**	**3′-end**
***p*-benzoquinone**	**5′-end**
benzoyl	**end+**

1.5 Format differences in headwords

The order for entries where the headword is identical except for format is

b, *b*, b-, *b*-, -b, -*b*, B, *B*, B-, *B*-, -B, -*B*

1.6 Subscripts and superscripts

Single letters with subscripts or superscripts are treated as single letters for the purposes of indexing, so entries for k_{cat} and K_m will both be found in the list of single-letter entries at the beginning of the letter K. The primary order of these single-letter entries is determined by their format (*see* section 1.5); where there is more than one entry with a given format (e.g. italic, lower case ***k***), these are arranged by alphabetical order of their subscripts/superscripts.

1.7 Greek letters

- Where Greek letters form part of a chemical name, they are not used to determine alphabetical order (*see* section 1.3). Otherwise they are written out in full in the headword, e.g. **nu body, beta strand.**
- The names of the letters of the Greek alphabet, together with their English transliterations used in etymologies, are listed in Appendix A. The meanings assigned to Greek alphabetic characters used as symbols are also given in Appendix A.
- Greek characters are set in italic type when the character represents a variable or locant and in roman type when it represents a unit or subtype e.g. of a protein or particle.

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2. Format of entries

2.1 Summary of typefaces

- The following distinguishing typefaces are employed in addition to the text light serif typeface used for definitions:

large bold sans serif	headwords
text bold serif	alternative terms for and variant spellings of headwords; hidden entries; run-ons
text bold sans serif	cross-references
text italic serif	usage notes and field labels; parts of speech; foreign language terms (including scientific and medical Latin); symbols for physical quantities and fundamental physical constants; stereochemical prefixes and alphabetical locants

2.2 Headwords

- For each entry, the headword is in bold, sans serif type.
- Upper-case (capital) initial letters are used only for proper names (or terms derived from them) and for proprietary names. Abbreviations and symbols are printed in upper and/or lower case as appropriate.
- If a term would normally be set in bold type, this is indicated in the entry:

  B *symbol for* **1** Napierian absorbance (*see* **absorbance**). **2** magnetic flux density (bold italic).
- Where the same basic term is used in different typefaces, such as roman/italic, or upper case/lower case, or as a prefix or suffix, each usage is given as a separate headword. For example, **h**, ***h***, **H**, and ***H*** each have a separate entry.
- The order in which such entries are given is listed in section 1.5.

2.3 Alternative terms and variant spellings

2.3.1 Choice of headword

Where alternative terms for a headword, or variant spellings of it, exist (*see* section 1.3), the headword selected for the main entry is generally the recommended or preferred term, or the one judged to be the commonest. Exceptions to this generalization are those instances where the name of a Greek alphabetic character is written out for convenience of indexing:

beta globulin *or* **β globulin**....

2.3.2 General

- Any alternative terms and alternative spellings are listed following the headword in bold, serif type:

  retrovirus *or* **ribodeoxyvirus** *or* **RNA–DNA virus** any virus belonging to the family Retroviridae....
- Notes regarding the usage of these alternatives may be given in brackets and in italics; for example

  DNA glycosylase *or (sometimes)* **DNA glycosidase** any of a group of enzymes....

  bacteremia *or (esp. Brit.)* **bacteraemia** the presence of live bacteria in the blood....

  bilirubin *or (formerly)* **bilirubin IXα** *the recommended trivial name for* the linear tetrapyrrole....
- These alternative terms and spellings also appear as entries in the alphabetical sequence, with a cross-reference to the main entry where the term is defined, unless the variant would appear close to the main entry. Additional information is given where appropriate:

  demoxytocin *an alternative name for* **deaminooxytocin**.

  fructose-1,6-diphosphatase *a former name for* **fructose-bisphosphatase**.

  lipide *a variant spelling of* **lipid**.

  molecular exclusion chromatography *a less common name for* **gel-permeation chromatography**.

  oleomargarine *an alternative name (esp. US) for* **margarine**.

  penatin *an obsolete name for* **glucose oxidase**.

2.3.3 Chemical names

- Synonyms may be given following the headword, in the order: other trivial names (if any); the semi-systematic or semi-trivial name(s); older systematic name in style, if still in widespread use; the systematic name in currently recommended style.
- The headword used to represent a chemical compound that can exist in ionized form(s) is in most cases the name of its physiologically predominant form. So, for example, an entry is headed 'succinate' rather that 'succinic acid'.

2.3.4 Enzyme names

Alternative names may be listed following the headword, which is normally the recommended name; otherwise alternative names include the recommended name (if the headword is the common name), the systematic name, and other names. The EC number is also given.

2.4 Multiple definitions

- Where a term has more than one meaning, the different senses are numbered with bold Arabic numerals.

  blockade **1** *(in pharmacology)* the saturation of a specific type of receptor with an antagonist to its normal agonist. **2** *(in immunology)* the overloading or saturation of the **reticuloendothelial system** with inert particles, such as carbon particles. **3** to impose any such blockade.
- The order of the numbered entries is generally determined by their biochemical significance.
- The different senses may be further subdivided into def. 1a, def. 1b, etc.

  di+ *comb. form* **1** *(in chemical nomenclature)* (*distinguish from* **bis+** (def. 2)) **a** indicating the presence in a molecule of two identical unsubstituted groups, e.g. diethylsulfide, 1,3-dihydroxyacetone. **b** indicating the presence in a molecule of two identical inorganic oxoacid residues in anhydride linkage, e.g. adenosine 5′-diphosphate. **2** *or* **bis+** (def. 1) denoting two, twofold, twice, doubled.
- Homographs are not distinguished.

2.5 Hidden entries

Hidden entries are terms that are not defined at their normal headword position. Instead, they are treated (implicitly or ex-

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plicitly) at some other headword. They are set in bold serif type. In the following example, 'bentonite flocculation test' is the hidden entry:

> **bentonite** a colloidal, native hydrated aluminium silicate clay consisting principally of montmorillonite, a complex aluminosilicate, $Al_2O_3 \cdot 4SiO_2 \cdot H_2O$, which has marked adsorptive properties. It is used as an inhibitor of nucleases and also in the **bentonite flocculation test**, a passive agglutination test in which antigen-coated bentonite particles are used to detect specific antibody.

2.6 Other information

2.6.1 Plurals

The plural form (or forms) of a headword is (are) given in parenthesis following the headword if its formation is non-standard, e.g. for Latin headwords, or where there is more than one form of the plural.

> **medulla** (*pl.* **medullas** *or* **medullae**) the innermost part of an organ, tissue, or structure; marrow, pith. — **medullary** *adj.*

2.6.2 Affixes and combining forms

- In common with other dictionaries, this Dictionary lists and defines many word elements that are used to compose terms or to modify existing terms. These are either combining forms (which are derived from parent words) or affixes (infixes, prefixes, and suffixes, none of which have parents).
- The usual lexicographical convention is to add a hyphen to suffixes and combining forms when listing them as headwords, although generally the hyphen is omitted in formation of composite terms. However, chemical and biochemical terminology also includes a considerable number of specialized affixes that retain the hyphen in the formation of composite terms (e.g. '*meso*-' in '*meso*-cystine').
  In order to make an explicit distinction between these alternatives, this Dictionary departs from the common convention by adding a hyphen to an affix in a headword only when a linking hyphen is retained in a combination:

  > ***meso-*** *abbr.*: *ms-*; *prefix* (*in chemical nomenclature*) designating a substance whose individual molecules contain....

  By contrast, combining forms (e.g., 'meso' in 'mesoderm') together with affixes producing unhyphenated composite terms, are listed with an added plus sign, placed after and/or before the word-element as appropriate:

  > **meso+** *or* (*sometimes before a vowel*) **mes+** *comb. form* denoting middle, or intermediate.
  >
  > **+agogue** *or* (*US*) **+agog** *suffix* denoting an agent that elicits or enhances the secretion of....

2.6.3 Abbreviations and symbols

- Where a term may be abbreviated or indicated with a symbol, this is noted after the headword.

  > **nuclear magnetic resonance** *abbr.*: NMR *or* nmr; the phenomenon that occurs when atomic nuclei....
  >
  > **electric potential** *or* **potential** *symbol*: *V or f*; the work done in bringing unit electric charge....

- The distinction between an abbreviation and a symbol is a little blurred, since some abbreviations (e.g. lg) also may be used as symbols. In general, the term 'symbol' is used here for

  - units and their decimal prefixes (e.g. m, mol; μ, M)
  - physical quantities and constants (e.g. *a*, *H*; *k*, *R*)
  - mathematical functions (e.g. exp, ln)
  - chemical elements (e.g. K, Mg)
  - groups of letters that can be used in place of a chemical group or compound in an equation or formula (e.g. CoA, Me)
  - recommended abbreviations for nucleotides, bases, or amino acids.

- The symbols for SI base and derived units and their decimal prefixes are mandatory; all other symbols are recommendations of IUBMB or IUPAC. In conformity with these recommendations, symbols for physical quantities and fundamental physical constants are printed in a sloping (italic) typeface.
- No distinction is made between acronyms, contractions, abbreviations, etc. All are classed as abbreviations. Abbreviations formed from the initial letters of two or more words are printed without periods (full-stops), in line with contemporary practice, but abbreviations that are shortened forms of single words have a terminal period.
- In addition to recommended abbreviations, the Dictionary lists a selection of others commonly encountered in the scientific literature.

2.6.4 Derived terms

Derived terms not meriting separate definition are listed at the end of the entry for the parent term, preceded by a bold em dash and followed by an abbreviation indicating the part of speech.

> **bactericide** *or* **bacteriocide** any agent (biological, chemical, or physical) that destroys bacteria. —**bactericidal** *or* **bacteriocidal** *adj.*

2.6.5 Etymology

- Generally, the derivation of words is not explained in entries. The exceptions are for eponymous terms and other entries of particular etymological interest.
- The etymology is given within square brackets at the end of the entry.

  > **ångström** *or* **Ångstrom** *symbol*: Å; a unit of length equal to 10^{-10} metres. ... [After Anders Jonas Ångström (1814–74), Swedish physicist noted for his work on spectroscopy.]

- Greek elements of etymologies are transliterated:

  > **chirality** topological handedness; the property of non-identity of an object with its mirror image. ... [From Greek *kheir*, hand.]

2.6.6 Usage

- The field within which the term is used may be specified in italics and in parenthesis before the definition.

  > **malonyl** **1** *(in biochemistry)* the univalent acyl group, $HOOC–CH_2–CO–$, derived from malonic acid by loss of one hydroxyl group. **2** *(in chemistry)* the bivalent acyl

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group, $-CO-CH_2-CO-$, derived from malonic acid by loss of both hydroxyl groups.

- Notes may also be given regarding the use of alternative terms and variant spellings: *see* section 2.3.2.

2.7 Cross-references

2.7.1 Format

- Cross-references are set in bold sans serif type, e.g. **thiouridine.**
- Where a cross-reference refers to only one sense of a word with multiple definitions, this is indicated as in the following example:

  siderophage *an alternative name for* **siderophore** (def. 1).

2.7.2 Types of cross-reference

- There are cross-references from a variant spelling, or a less commonly used term, etc., to the entry where the term is defined. For examples, *see* section 2.3.2.
- Some cross-references are to related entries giving more information. These may be either embedded in the text:

  octulose any **ketose** having a chain of eight carbon atoms in the molecule.

  or listed at the end of the entry:

  vacuum evaporation a technique for .... *See also* **shadow casting**.
- Cross-references may also be used to draw attention to contrasting terms:

  heterochromatin ... *Compare* **euchromatin**.

  or to pairs of easily confused terms:

  prolidase *another name for* **X-Pro dipeptidase**. *Distinguish from* **prolinase**.

  prolinase *the recommended name for* **Pro-X dipeptidase**. *Distinguish from* **prolidase**.

3. Abbreviations

abbr.	abbreviation
adj.	adjective
adv.	adverb
Brit.	British
comb. form	combining form (*see* section 2.6.2)
3-D	three-dimensional
def.	definition
e.g.	[Latin, *exempli gratia*] for example
esp.	especially
etc.	etcetera
Fr.	French
i.e.	[Latin, *id est*] that is
max.	maximum
n.	noun
pl.	plural
sing.	singular
sp. or spp.	species (singular and plural respectively)
US	United States
vb.	verb

Other abbreviations are defined in the text itself.

4. Other conventions

4.1 Spelling and hyphenation

4.1.1 Spelling

- For chemical and biochemical terms, recommended international usage is followed; thus, for example, 'heme' is used rather than 'haem', 'estrogen' rather than 'oestrogen', 'sulfur' rather than 'sulphur', and 'oxytocin' rather than 'ocytocin'. All variants are listed as headwords, however, with cross-references to the corresponding main entries.
- For common terms, e.g. 'colour', British spelling is used.

4.1.2 Hyphenation

- Hyphens are used attributively:

  'T cell' but 'T-cell receptor'

  'amino acid' but 'amino-acid residues'
- This also applies to enzyme names; thus for example, there is no hyphen following the 'glucose' in 'glucose 6-phosphate', but where this substrate forms part of an enzyme name, it is hyphenated, e.g. in 'glucose-6-phosphatase' or 'glucose-6-phosphate isomerase'.

4.2 Nomenclature

In most cases, headwords conform with the recommendations of the various nomenclature bodies of IUB, IUBMB, and IUPAC (*see* Appendix B for information regarding their nomenclature publications). Other usages are, however, given (*see* Preface). The phrase 'not recommended' has been used to indicate that certain forms are not the recommendation of one of these nomenclature bodies.

4.2.1 Drug names

The recommended international nonproprietary names are used (*International nonproprietary names (INN) for pharmaceutical substances*. World Health Organization, Geneva, 1992); hence, for example, main entries are found under epinephrine and norepinephrine rather than under adrenaline and noradrenaline.

4.2.2 Proprietary names

A few commonly used proprietary names are included; these may be listed at the end of an entry if considered to be of particular interest, especially to non-scientists:

acetaminophen *or* **paracetamol** ... *Proprietary names:* Tylenol, Panadol. It inhibits ....

or may be the main headword:

Sephadex.

4.2.3 Other substances

The main entry is under the name used most widely in the scientific literature. Where this is not the recommended name, a cross-reference is given from the recommended name to the main entry. For example, the name 'follicle-stimulating hormone (FSH)' is widely employed instead of the recommended name 'follitropin', hence the former name has been used as the main headword. In such cases there is a cross-reference from the recommended name back to the entry where the substance is defined:

follitropin *the recommended name for* **follicle-stimulating hormone**.

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4.3 Representation of chemical structures

4.3.1 Typeset formulae

In conformity with IUPAC nomenclature recommendations for typeset chemical formulae, parentheses (round brackets) indicate a side chain:

$CH_3–CH(NH_2)–COOH$,

$HO–C(CH_2–COO^-)_2–COO^-$

and square brackets indicate a condensed chain:

$CH_3–[CH_2]_8–COOH$

4.3.2 Carbohydrates

- The cyclic forms of monosaccharides are depicted by Haworth representations as are some other compounds; for clarity, the carbon atoms of the heterocyclic ring, and their attached hydrogen atoms, are not shown. *See* the **Haworth representation** entry for more detail.
- Where an abbreviated terminology is included for oligosaccharide chains, the extended or condensed forms described in the publication entitled *Nomenclature of carbohydrates (recommendations 1996)* (*see* Appendix B, item 22) are variously used.
- Wherever possible, structure diagrams show absolute configurations.

4.4 Periodic table of the elements

The group numbers used in the text are those of the 18-column format of the table given in the 1990 edition of the IUPAC 'Red Book' (*see* Appendix B, item 2). The correspondence between this and other versions of the table is described in the **periodic table** entry and shown below the table displayed on the endpapers.

4.5 Amino-acid sequences

- For peptide sequences of up to 15 amino-acid residues, the three-letter code is used; longer sequences are given in the one-letter code.
- Motifs are given in the one-letter code.
- The full sequences of many proteins can be found in protein sequence databases, and database codes are given to facilitate access to these. The database codes relate to a number of different databases. The style of the code gives an indication of the database from which the data originate, but if the user does not recognize the code, it is necessary to search for it in a composite database that integrates data from all the major databases. Further information is offered in Appendices D and E.

4.6 Genes

- The accepted format of gene names (i.e., whether lower case or upper case or a mixture) varies between different organisms. Where an entry covers genes from various species, the convention for human genes is generally followed in the headword, i.e. all letters are given in upper case, e.g. '*JUN*'.
- However, when an entry refers only to a gene from a specified organism, the accepted convention for that organism is followed.

4.7 Names of organisms

- Those organisms whose Latin names are used frequently are listed in Appendix H.
- Where a binomial Latin name is repeated within an entry, the genus name is abbreviated after the first occurrence of the name; for example, the full form '*Escherichia coli*' is used when first mentioned in any entry, but subsequent references to this organism in the same entry are abbreviated to '*E. coli*'.

5. Appendices

A number of appendices have been included after the main alphabetical text, as follows:

- Appendix A – The Greek alphabet and Greek characters used as symbols (page 697).
- Appendix B – Nomenclature publications (page 700).
- Appendix C – Organizations that are helpful to biochemists and molecular biologists (page 705).
- Appendix D – The Internet (page 709).
- Appendix E – Exploring the language of bioinformatics (page 715).
- Appendix F – Restriction enzymes and methylases (page 725).
- Appendix G – Sequence-rule priorities of some common ligands in molecular entities (page 739).
- Appendix H – Species names (page 740).

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Aa

a 1 *abbr. for* adsorbed. 2 *symbol for* atto+ (SI prefix denoting 10^{-18}). 3 axial. 4 year.

a' *symbol for* pseudoaxial.

a *symbol for* 1 absorption coefficient. 2 acceleration (in vector equations it is printed in bold italic (***a***)). 3 activity (def. 3). 4 van der Waals coefficient. 5 *as subscript*, denotes affinity.

a_0 *symbol for* Bohr radius.

A *symbol for* 1 acid-catalysed (of a reaction mechanism). 2 a residue of the α-amino acid L-alanine (alternative to Ala). 3 a residue of the base adenine in a nucleic-acid sequence. 4 a residue of the ribonucleoside adenosine (alternative to Ado). 5 uronic acid. 6 ampere.

A *symbol for* 1 absorbance. 2 activity (def. 2). 3 affinity. 4 Helmholtz function. 5 mass number/nucleon number.

A_r *symbol for* relative atomic mass.

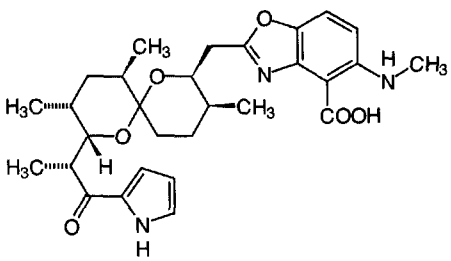
A_s *symbol for* area.

$[A]_{0.5}$ *or* **$[A]_{½}$** *symbol (in enzyme kinetics) for* the value of the concentration of a substrate, A, in mol dm^{-3}, at which the velocity of the reaction, v, is half the maximum velocity, V; i.e. when $v = 0.5V$.

$[A]_{50}$ *symbol for* the molar concentration of an agonist that produces 50% of the maximal possible effect of that agonist. Other percentage values ($[A]_{20}$, $[A]_{40}$, etc.) can be specified. The action of the agonist may be stimulatory or inhibitory. *Compare* **EC_{50}**.

2′-5′A *symbol for* any member of a series of oligonucleotides of the general formula $p_aA[2'p5'A]_n$, where p and A are phosphoric and adenosine residues, respectively, and a and n are small integers (a = 1, 2, or 3 and n commonly = 2, 3, or 4). Potent inhibitors of protein biosynthesis *in vivo* and *in vitro*, they are believed to mediate the action of interferon on virus-induced cells.

A23187 *or* **calcimycin** a toxic and weakly antibiotic substance isolated from cultures of *Streptomyces chartreusensis*. It is a lipophilic 523 Da monocarboxylic acid of complex structure, two molecules of which form stable lipid-soluble complexes at pH 7.4 with one atom of certain divalent metal cations, especially Mn^{2+}, Ca^{2+}, and Mg^{2+}; monovalent cations are bound only weakly. It also forms lipid-soluble complexes with certain amino acids. It is used experimentally as a calcium **ionophore**.



Å *symbol for* ångström (unit of length equal to 10^{-10} m).

aa 1 *symbol for* an unknown or unspecified aminoacyl group when acting as a substituent on a base or internal sugar in a (poly)nucleotide. 2 *abbr. for* amino acid.

AA *(formerly) symbol for* an unknown or unspecified amino-acid residue. *See* **Xaa**.

AAA a codon in mRNA for L-lysine.

AAC a codon in mRNA for L-asparagine.

Aad *symbol for* a residue of the α-amino acid L-α-aminoadipic acid, L-2-aminohexanedioic acid.

βAad *symbol for* a residue of the β-amino acid L-β-aminoadipic acid, L-3-aminohexanedioic acid.

AAG a codon in mRNA for L-lysine.

A antigen the antigen defining the A blood group. *See also* **blood-group substance, ABH antigens**.

AAU a codon in mRNA for L-asparagine.

Ab *abbr. for* antibody.

abamectin *or* **avermectin B_1** a metabolite of *Streptomyces avermitilis* used as an acaricide, insecticide, and a veterinary anthelmintic.

A-band an anisotropic band in a **sarcomere**.

Abbe refractometer a **refractometer** in which the critical angle for total reflection at the interface of a film of liquid between two similar glass prisms is used in determining the refractive index of the liquid. [After Ernst Abbe (1840–1905), German physicist famous for his researches in optics.]

ABC *abbr. for* 1 antigen-binding capacity. 2 ATP-binding cassette (*see* **ABC transporter**).

ABC transporter membrane transport proteins having the ABC molecular domain, named after ATP-binding cassette, characteristic of all members of a large superfamily of membrane transport proteins that hydrolyse ATP and transfer a diverse array of small molecules across membranes. *See also* **CFTR, MDR protein, sugar transporter**.

abductin an insoluble, rubber-like protein from the internal triangular hinge ligament of scallops.

Abe *symbol for* abequose.

abequose *symbol*: Abe; 3,6-dideoxy-D-*xylo*-hexose; 3,6-dideoxy-D-galactose; a deoxysugar that occurs, e.g., in O-specific chains of lipopolysaccharides in certain serotypes of *Salmonella*. For the L enantiomer *see* **colitose**.

ABH antigens one of the systems of **blood group** antigens having determinants associated with oligosaccharide structures. It is the basis of the **ABO system**, which was the first human blood group antigen system to be detected, by Landsteiner in 1901, and it remains the most important in blood transfusion. Individuals having neither A nor B antigen express the H antigen, the product of an independent gene belonging to the Hh system. Antigens of the ABH system are oligosaccharide chains, in the erythrocyte carried on band 3 (the anion transporter) and band 4.5 (the glucose transporter), or on ceramide. A highly branched *N*-glycan, consisting of a trimannosyl-di-*N*-acetyl-chitobiosyl core with Gal(β1-4)GlcNAc(β1-3) repeats, forms the basis of ABH antigens. The H determinant is the precursor; antigen A is formed by addition of *N*-acetyl-D-galactosamine by fucosylgalactose α-*N*-acetylgalactosaminyltransferase (EC 2.4.1.40); antigen B is formed by addition of D-galactose by fucosylglycoprotein 3-α-galactosyltransferase (EC 2.4.1.37). The terminal sugar residues of importance are: H determinant, Fuc(α1-2)Galβ-R; A determinant, GalNAc(α1-3)(Fucα1-2)Galβ-R; B determinant, Gal(α1-3)(Fucα1-2)Galβ-R. The enzyme responsible for adding the terminal fucosyl residue of the H determinant is galactoside 2-α-L-fucosyltransferase (EC 2.4.1.69). *See also* **A-transferase, B-transferase**.

abiogenesis *or* **spontaneous generation** the discredited doctrine that living organisms can arise from nonliving materials under current conditions. *Compare* **biogenesis** (def. 2).

abiotic characterized by the absence of life.

abl an oncogene from murine Abelson leukemia virus. The viral oncogene (v-*abl*) resulted from recombination of the Maloney murine leukemia virus with the protooncogene (c-*abl*). The protooncogene encodes a 145 kDa protein, which, together with the highly related *arg* gene, forms a unique family within the nonreceptor tyrosine protein kinases; database code KABL_HUMAN. 1130 amino acids (122.81 kDa). It was one

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of the first protooncogenes identified by the study of retroviruses. The transforming ability of v-*abl* results from increased tyrosine kinase activity of the *gag–abl* p160 oncoprotein. In humans, inappropriate activation of c-*abl* occurs via a reciprocal translocation between chromosomes 9 and 22 in which c-*abl* (9q34) is joined at the **breakpoint cluster region** (bcr) of the *ph1* gene on chromosome 22(q11). In the translocation, a 3′ portion of c-*abl* is spliced in-frame to a 5′ portion of the *ph1* gene, resulting in an altered chromosome 22, which is referred to as the **Philadelphia chromosome** (Ph^1). The protein product of the spliced genes in the Ph^1 chromosome is a molecule of 210 kDa, which has increased tyrosine kinase activity compared with the c-*abl* product and is similar in structure to the v-*abl* product in that the N-terminal portion of Abl is removed. The Ph^1 chromosome occurs in more than 90% of individuals with chronic myelogenous leukemia and was the first description of a specific genetic translocation associated with a human malignancy. c-Abl can potentially regulate cell growth and may participate in growth regulation at multiple cellular locations, interacting with different cell components. It possesses SH2 and SH3 domains (*see* **SH domains**) and also domains involved in binding to F-actin and DNA. Thus it has been found in both cytoplasmic and nuclear locations and its DNA-binding activity appears to be cell cycle regulated by Cdc-2-mediated phosphorylation; it binds the **retinoblastoma protein** indicating involvement in transcriptional regulation.

ABM *abbr. for* 2-aminobenzyloxymethyl, a group used for derivatizing cellulose or paper. It is converted by diazotization into **DBM**.

abortive complex *or* **dead-end complex** *or* **nonproductive complex** any enzyme–substrate complex in which the substrate is bound to the enzyme in a manner that renders catalysis impossible so that products cannot be formed.

abortive infection infection of a bacterium by phage lacking phage DNA, e.g. in generalized **transduction**.

abortive transconjugate *see* **transconjugate**.

abortive transduction a type of **transduction** in which the donor DNA is not integrated with the recipient chromosome but persists as a nonreplicating fragment that can function physiologically and can be transmitted to one daughter cell at each cell division.

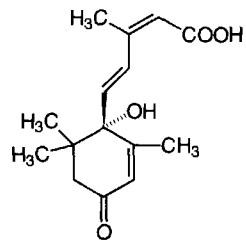
ABO system one of the systems of human **blood groups**, of great importance in blood transfusion because human plasma contains natural antibodies against A and B blood group antigens of the ABH system (*see* **ABH antigens**). The antigens on the red blood cells and the plasma antibodies corresponding to the various phenotypes are shown in the table. *See also* **A-transferase**, **B-transferase**, **O antigen** (def. 2).

Phenotype (blood group)	Antigen on red cells	Antibody in plasma
A	A	anti-B
B	B	anti-A
AB	A and B	neither
O	H	anti-A + anti-B

abrin a highly toxic ≈65 kDa glycoprotein obtained from the seeds of jequirity or Indian liquorice (*Abrus precatorius* L.), a tropical Asian vine that also occurs in Florida. It consists of an acidic A chain, ≈30 kDa, and a neutral B chain, ≈35 kDa, held together by disulfide bonds. The A chain is a powerful inhibitor of protein synthesis while the B chain functions as a carrier to bind abrin to the membrane and perhaps to assist penetration of the A chain into the cell. One well-chewed seed can be fatal. The A and B chains are derived from a common precursor: database code ABRA_ABRPR, 528 amino acids (59.24 kDa). *Compare* **abrine**, **ricin**. *See also* **ribosome-inactivating protein**.

abrine *trivial name for* N^{α}-methyl-L-tryptophan, α-methyl-amino-β-(3-indole)propionic acid; an imino acid obtained from seeds of jequirity (*Abrus precatorius*). Not to be confused with **abrin**.

abscisic acid *or (formerly)* **abscisin II** *or* **dormin** *abbr.*: ABA; 5-(1-hydroxy-2,6,6-trimethyl-4-oxocyclohex-2-en-1-yl)-3-methylpenta-2,4-dienoic acid; a chiral sesquiterpene. The naturally occurring form, the 2*Z*,4*E*,*S* isomer, also designated (*S*)-abscisic acid, is a phytohormone formed by the degradation of carotenoids. It controls abscission in flowers and fruit but probably not in leaves, and is also implicated in geotropism, stomatal closure, bud dormancy, dormancy of seeds requiring stratification (i.e. those that will only germinate after exposure to low temperatures), and possibly tuberization.



abscissa the horizontal or *x* coordinate in a plane rectangular (Cartesian) coordinate system. *Compare* **ordinate**.

abscission the natural shedding of leaves, fruits, and other parts by a plant.

absolute **1** pure, unmixed; e.g. absolute alcohol. **2** not relative; e.g. absolute configuration. **3** describing a measurement defined in fundamental units of mass, length, and time that does not depend on the characteristics of the measuring apparatus; e.g. absolute temperature.

absolute alcohol *the common name for* pure ethanol, i.e. ethanol that has been freed of water. It may contain small amounts of benzene that have been added to aid in removing water. Substances may be added to absolute alcohol to render it unfit for human consumption and hence free of excise duty: **industrial spirit** contains 5% v/v methanol, while **methylated spirit** also contains pyridine, petroleum oil, and methyl violet dye, and **surgical spirit** also contains castor oil, diethyl phthalate, and methyl salicylate.

absolute configuration the actual three-dimensional arrangement of the atoms in a chiral molecule.

absolute reaction rate theory a theory that sets out to predict the absolute reaction rate of a chemical reaction from the quantum mechanical description of the potential energy changes during the interaction between chemical species. It is most widely drawn upon in applying thermodynamic reasoning to equilibria between reactants in the ground state and chemical species in the activated state or transition state.

absolute temperature *see* **thermodynamic temperature**.

absolute zero zero **thermodynamic temperature**, i.e. 0 K or −273.15 °C.

absorb *see* **absorption**.

absorbance *symbol*: *A*; a measure of the ability of a substance or a solution to absorb electromagnetic radiation incident upon it. It equals the logarithm of the ratio of the radiant power of the incident radiation, Φ_0, to the radiant power of the transmitted radiation, Φ. For a solution, absorbance is expressed as the logarithm of the ratio of the radiant power of light transmitted through the reference sample to that of the light transmitted through the solution, the observations being made using identical cells. (Traditionally, radiant intensity was measured instead of radiant power, which is now the accepted form.) Two quantities are defined: **(decadic) absorbance** (*symbol*: A_{10} *or* A), and **napierian absorbance** (*symbol*: A_e *or* B).

$$A_{10} = \lg (\Phi_0/\Phi) = \lg T^{-1} = -\lg (1 - \alpha), \text{ and}$$

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$$A_e = \ln(\Phi_0/\Phi) = \ln T^{-1} = -\ln(1-\alpha),$$

where T is the (internal) **transmittance** and α is the **absorptance**. These definitions suppose that all the light incident upon the sample is either transmitted or absorbed, reflection and scattering being negligible. The more general term attenuance should be used when scattering is considerable, as when the quantity $\lg(\Phi_0/\Phi)$ is measured to estimate the cell density of a culture. The older terms **absorbancy**, **extinction**, and **optical density** should no longer be used. *Compare* **absorption coefficient**.

absorbancy *or* **absorbency** *(formerly) an alternative term (no longer recommended) for* **absorbance**.

absorbate a substance that is absorbed into another substance.

absorbed dose *(in radiation physics)* a measure of the energy deposition produced by **ionizing radiation** in any (specified) medium as a result of **ion-pair** formation. The CGS unit of absorbed dose is the **rad**; the SI derived unit is the **gray** (*symbol*: Gy); *compare* **exposure** (def. 3). *See also* **dose equivalent**, **dose rate**.

absorbence *a variant spelling of* **absorbance**.

absorbent **1** a substance that absorbs another substance. **2** having the capacity to absorb another substance.

absorptance *or* **absorption factor** *symbol:* α; the ratio of absorbed to incident radiant or luminous flux. A dimensionless physical quantity given by $\alpha = \Phi_{abs}/\Phi_0$, where Φ_0 and Φ_{abs} are the incident and absorbed radiant powers, respectively.

absorptiometer **1** an apparatus, frequently a photoelectric device, for measuring light **absorption** by solids, liquids, or gases. **2** an apparatus for measuring the amount of gas absorbed by a liquid.

absorption **1** the act or process whereby one substance, such as a gas or liquid, is taken up by or permeates another liquid or solid. *Compare* **adsorption**. **2** the retention by a material of energy removed from electromagnetic radiation passing through the material. **3** the removal of any form of radiation, or the reduction of its energy, on passing through matter. **4** the process whereby a neutron or other particle is captured by an atomic nucleus. **5 a** *(in cellular physiology)* the uptake of fluids by living cells or tissues. **b** *(in animal physiology)* the totality of the processes involved in causing water, the products of digestion, and exogenous substances of low molecular mass such as drugs, salts, vitamins, etc. to pass from the lumen of the gastrointestinal tract into the blood and lymph. **c** *(in plant physiology)* the uptake of water and dissolved salts through the roots. **6** *(in immunology)* the process of removing a particular antibody (or antigen) from a mixture by adding the complementary antigen (or antibody) and discarding the antigen–antibody complex so formed. *Compare* **immunosorption**.

absorption band *or* **absorption line** a region of darkness or absorption of radiation in the spectrum of heterochromatic radiation that has passed through an absorbing material.

absorption coefficient four different coefficients are defined. The **(linear) decadic absorption coefficient** (*symbol*: a) is defined by $a = A_{10}/l$; units m^{-1}. The **(linear) napierian absorption coefficient** (*symbol:* α) is defined by $\alpha = A_e/l$; units m^{-1}. The **molar (decadic) absorption coefficient** (*symbol:* ε) is defined by $\varepsilon = a/c = A_{10}/cl$; units $m^2\,mol^{-1}$. The **molar napierian absorption coefficient** (*symbol:* κ) is defined by $\kappa = \alpha/c = A_e/l$. A_{10} and A_e are the decadic and napierian absorbances respectively (*see* **absorbance**), l = path length, and c = amount-of-substance concentration.

absorption cross-section the probability that a photon passing through a molecule will be absorbed by that molecule multiplied by the average cross-sectional area of the molecule. The **net absorption cross-section** (*symbol:* σ_{net}) is defined by $\sigma_{net} = \kappa/N_A$, where κ is the molar napierian **absorption coefficient** and N_A is the Avogadro constant.

absorption factor *an alternative name for* **absorptance**.

absorption index *symbol:* k; it is given by $k = \alpha/4\pi\tilde{\nu}$, where α is the (linear) napierian **absorption coefficient** and $\tilde{\nu}$ the wavenumber in vacuum of the radiation.

absorption line *an alternative name for* **absorption band**.

absorption spectrometry the process of measuring an absorption spectrum with a **spectrometer**. **Absorption spectrophotometry** is a related process employing a spectrophotometer. *See also* **absorbance**, **absorptivity**.

absorption spectroscopy the **spectroscopy** of an absorption spectrum.

absorption spectrum a **spectrum** produced when electromagnetic radiation is absorbed by a sample. The frequencies of the radiation absorbed are those able to excite the atoms or molecules of the sample from their ground states to excited states. The frequency, ν, at which a particular absorption line occurs depends on the energy difference, ΔE, between that of a particular ground state and that of the corresponding excited state. It is given by $\nu = \Delta E/h$, where h is the Planck constant. *Compare* **emission spectrum**.

absorptivity a measure of the ability of a material to absorb electromagnetic radiation. It equals the absorptance of a sample of the material divided by the optical path-length. For very low attenuance, it approximates the absorption coefficient. Use of the term is not recommended.

Abu *symbol for* a residue of the α-amino acid L-2-aminobutanoic acid L-α-aminobutyric acid.

A_2bu *or* **Dab** *symbol for* a residue of the α,γ-diamino acid L-α,γ-diaminobutyric acid, L-2,4-diaminobutanoic acid.

abzyme *abbr. for* antibody enzyme (an antibody with enzyme activity; also known as catalytic monoclonal antibody).

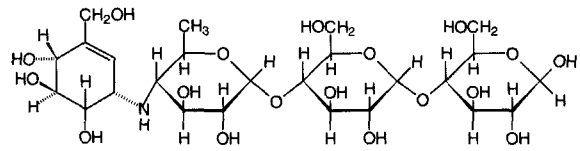
a.c. *or* **AC** *or* ***ac*** *abbr. for* alternating current.

Ac *symbol for* **1** actinium. **2** the acetyl group, $CH_3CO–$.

ACA a codon in mRNA for L-threonine.

acanthosome an organelle of fibroblasts isolated from the dermis of hairless mice after chronic UV irradiation. It exists as a spinous membranous vesicle.

acarbose a pseudotetrasaccharide, *O*-4,6-dideoxy-4-[[[1*S*-(1α,4α,5β,6α)]-4,5,6-trihydroxy-3-(hydroxymethyl)-2-cyclohexen-1-yl]amino]-α-D-glucopyranosyl-(1→4)-*O*-α-D-glucopyranosyl-(1→4)-glucose, that inhibits α-glucosidase, thereby reducing gastrointestinal absorption of glucose. It is a putative antidiabetic agent.



ACC a codon in mRNA for L-threonine.

a.c. calorimetry a technique in which the thermal response of a sample to an oscillating heat signal is measured in the form of a temperature wave propagating through the sample. The technique allows the measurement of the heat capacity of the sample on both cooling and heating and the monitoring of its isothermal time-dependence. It is useful in the study of phase transitions in solids and in gel to liquid-crystal systems.

accelerator **1** *(in chemistry)* **catalyst**, especially one that increases the rate of a polymerization reaction. **2** *(in physics)* a device or machine used for imparting high kinetic energy to charged subatomic particles, e.g. electrons, protons, or alpha particles, by means of electric and/or magnetic fields.

accelerator globulin *an alternative name for* factor V. *See* **blood coagulation**.

accelerin *an alternative name for* factor Va. *See* **blood coagulation**.

acceptor **1** *(in chemistry)* a chemical entity that in a chemical reaction receives an electron, atom, or group of atoms. *Compare* **donor**, **donor atom**. *See also* **electron acceptor**. **2** *(in physiol-*

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ogy) a receptor that binds a hormone without a biological response being demonstrable. **3** *(in pharmacology)* a receptor that binds a drug but has no identified endogenous ligand.

accessory cell any one of various types of cell that assist in the immune response. The term includes **antigen-presenting cell**, **basophil**, **eosinophil**, **mast cell**, and **platelet**.

accessory chromosome *an alternative name for* **1** a **B chromosome**. **2** a **sex chromosome**.

accessory DNA surplus DNA present in certain cells or during certain stages of cell development owing, for example, to **gene amplification**.

accessory food factor *or* **accessory growth factor** a term originally used to describe any unknown substance – subsequently called **vitamin** – found in small amounts in some foods, such as milk, that was necessary for the normal growth of animals fed on diets of purified carbohydrates, fats, proteins, and salts.

accessory pigment any of the pigments, such as the yellow, red, or purple **carotenoids** and the red or blue **phycobiliproteins** in photosynthetic cells. The carotenoids are always present, whereas the phycobiliproteins occur only in algae belonging to the Rhodophyceae, the Cyanophyceae, and the Cryptophyceae. Strictly speaking, chlorophyll b is also an accessory pigment.

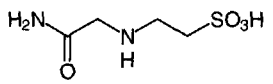
ACE *abbr. for* **1** amplification control element (a DNA sequence in vertebrates that functions as the origin for **amplification**). **2 angiotensin converting enzyme**.

ACeDB *or* **acedb** a partly object-oriented database of genetic and sequence information devised for the nematode *Caenorhabditis elegans* but applied to other eukaryotes including *Arabidopsis thaliana*.

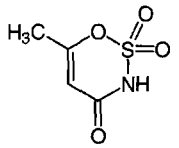
A cell *or (formerly)* **alpha cell** *or* **α cell** one of the three main histological cell types found in the islets of Langerhans of the pancreas, also found in the gastric oxyntic mucosa. A cells produce, store, and secrete the hormone **glucagon**.

A_1 cell *(formerly) an alternative name for* **D cell**.

Aces *or* **ACES** *abbr. for N*-(2-acetamido)-2-aminoethane sulfonic acid; 2-[(2-amino-2-oxoethyl)amino]ethane sulfonic acid; a **Good buffer substance**, pK_a (20 °C) = 6.9.



acesulfame 6-methyl-1,2,3-oxathiazin-4(3*H*)-one 2,2′-dioxide; a sweet-tasting material that, as the potassium salt, has been used in foods and cosmetics.



acetal any member of a class of organic compounds having the general formula $R^1HC(OR^3)OR^4$ or $R^1R^2C(OR^3)OR^4$ – in a **thioacetal** the corresponding formulae are $R^1HC(SR^3)SR^4$ or $R^1R^2C(SR^3)SR^4$ – where R^3 and R^4 are alkyl groups (or R^4 is H in a **hemiacetal** or **hemithioacetal**). An acetal molecule is formed by the acid-catalysed combination of the carbonyl group of an aldehyde or ketone molecule with either one or two alcohol (or mercaptan) molecules (which may be the same or different), or with a diol (or dithiol), by a reaction of the following general type, where X is O (or S in a mercaptan or dithiol):

$$R^1R^2C{=}O + R^3XH = R^1R^2C(XR^3)OH.$$

The hemiacetal (or hemithioacetal) so formed may then undergo a further reaction

$$R^1R^2C(XR^3)OH + R^3XH = R^1R^2C(XR^3)_2 + H_2O$$

or

$$R^1R^2C(XR^3)OH + R^4XH = R^1R^2C(XR^3)XR^4 + H_2O.$$

In carbohydrates such compounds are formed at the carbonyl group of the acyclic form of a saccharide or saccharide derivative. The terms 'ketal' (or 'thioketal') and 'hemiketal' (or 'thiohemiketal'), may be applied respectively to any acetal of general formula $R^1R^2C(XR^3)XR^4$ or $R^1R^2C(OH)XR^3$, i.e. to those derived from ketones. These terms, at one time abandoned, have recently been reintroduced as the respective names of subclasses of acetals and hemiacetals and as functional class names.

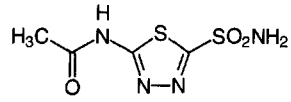
acetaminophen *or* **paracetamol** 4-acetamidophenol; *N*-acetyl-*p*-aminophenol; *N*-(4-hydroxyphenyl)acetamide; a drug widely used as an analgesic and antipyretic. It inhibits formation of prostaglandins within, but not outside the brain. It is metabolized within the liver mostly to glucuronide and sulfate conjugates. A small amount is oxidized to a highly reactive intermediate, *N*-acetylbenzoquinoneimine, that is normally detoxified by conjugation with glutathione. If it is produced in excess of the capacity of the liver to detoxify it, hepatic necrosis can result. It can be administered with methionine, which increases glutathione in the liver. *N*-Acetylcysteine is administered in cases of poisoning to act as a glutathione substitute. *Proprietary names include*: Panadol, Tylenol.

acetate **1** the traditional name for ethanoate; the anion, CH_3COO^-, derived from acetic acid (ethanoic acid). **2** any salt or ester of acetic acid.

acetate–CoA ligase EC 6.2.1.1; *systematic name*: acetate:CoA ligase (AMP-forming); *other names*: acetyl–CoA synthetase; acyl-activating enzyme; acetate thiokinase; acetyl-activating enzyme. An enzyme that catalyses a reaction between ATP, acetate, and CoA to form AMP, pyrophosphate, and acetyl-CoA. It is an important enzyme in organisms (e.g. *Escherichia coli*, many fungi, protozoans, algae) that utilize acetate as a carbon source. Example from *E. coli*: database code ACUA_ECOLI, 652 amino acids (72.01 kDa). Distinguish from acetate–CoA ligase (ADP-forming), EC 6.2.1.13.

acetate thiokinase *see* **acetate–CoA ligase**.

acetazolamide an inhibitor of carbonic anhydrase that is useful as a diuretic. It acts by preventing bicarbonate reabsorption in the proximal tubules of the kidney.



(+)aceto+ *comb. form* denoting the acyl group derived from acetic acid.

acetoacetate–CoA ligase EC 6.2.1.16; *other name*: acetoacetyl-CoA synthetase; an enzyme that catalyses the formation of acetoacetyl-CoA from ATP, acetoacetate, and CoA with release of AMP and pyrophosphate. In bacteria that carboxylate acetone to acetoacetate, it activates the latter for further metabolism. It is also present in animals, but utilization of blood acetoacetate after its entry into tissues involves **3-oxoacid CoA-transferase**.

acetoacetyl acetyltransferase *see* **acetyl-CoA *C*-acetyltransferase**.

acetoacetyl-CoA synthetase *see* **acetoacetate–CoA ligase**.

acetoacetyl-CoA thiolase *see* **acetyl-CoA *C*-acetyltransferase**.

acetogenin any substance built up of two-carbon units that may formally be considered to derive from a polyacetyl chain intermediate; the carbon atoms derived from the carboxyl carbon atoms of acetic acid frequently remain oxidized. It is not a recommended term. *See* **polyketide**.

acetoin 3-hydroxy-2-butanone; accompound formed by action

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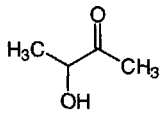
of acetolactate decarboxylase (EC 4.1.1.5) and, under some conditions, pyruvate decarboxylase (EC 4.1.1.1).



acetone body *see* **ketone body**.

acetone powder any preparation of ruptured cells obtained from a tissue or single-celled organisms that involves dehydration with acetone to form a powder. It is relatively stable, and is used in the preparation of some enzymes.

acetyl the acyl group ethanoyl, $CH_3CO–$, derived from acetic acid (= ethanoic acid).

acetylation an **acylation** reaction in which an acetyl group, $CH_3CO–$, is introduced into an organic compound. —**acetylated** *adj.*

acetylation coenzyme *the original name for* **coenzyme A**.

acetylcholine receptor *see* **cholinoceptor**.

acetylcholinesterase *abbr.*: AChE; EC 3.1.1.7; *systematic name*: acetylcholine acetylhydrolase; *other names*: true cholinesterase; cholinesterase I; an esterase enzyme that catalyses the hydrolysis of acetylcholine to choline and acetate; it also acts on a variety of acetic esters and catalyses transacetylations. It is found in or attached to cellular or basement membranes of presynaptic cholinergic neurons and postsynaptic cholinoceptive cells. A soluble form occurs in cerebrospinal fluid and within cholinergic neurons. It is inhibited by a number of drugs, e.g. physostigmine, and by several **organophosphates**. Example from human: database code ACES_HUMAN, 614 amino acids (67.72 kDa). The 3-D structure is known for fragments obtained from the electric ray (fish).

acetylcholine transporter protein an integral membrane protein of synaptic vesicles of cholinergic neurons. It transports newly synthesized acetylcholine molecules into the synaptic vesicles in exchange for protons, thereby replenishing vesicular stores of the neurotransmitter. Example from *Caenorhabditis elegans*: database code UN17_CAEEL, 532 amino acids (58.58 kDa).

acetyl-CoA *abbr. for* **acetyl coenzyme A**.

acetyl-CoA *C*-acetyltransferase EC 2.3.1.9; *other names*: acetoacetyl acetyltransferase; acetoacetyl-CoA thiolase; an enzyme that catalyses the formation of two molecules of acetyl-CoA from CoA and acetoacetyl-CoA. During beta oxidation it catalyses the formation of acetyl-CoA from acetoacetyl-CoA, whereas it acts in the reverse direction to form acetoacetyl-CoA during ketogenesis. It is important in regulating the metabolic pathways for the production of acids, i.e. acetate, butyrate, or solvents, i.e. acetone, butanol, ethanol, during the growth of *Clostridium acetobutylicum*. Reduced activity of the enzyme favours production of acetate and ethanol, while increased activity favours production of butyric acid, butanol, and acetone. Example from human (mitchondrial, precursor): database code THIL_HUMAN, 427 amino acids (45.15 kDa).

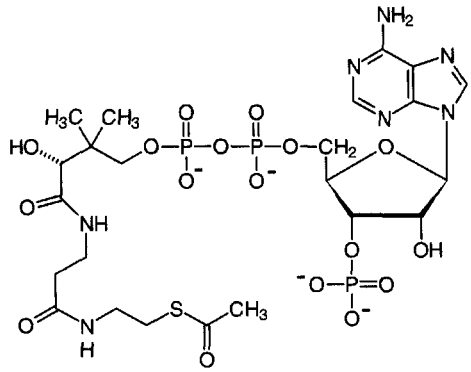
acetyl-CoA *C*-acyltransferase EC 2.3.1.16; *systematic name*: acyl-CoA:acetyl-CoA *C*-acyltransferase; *other names*: 3-ketoacyl-CoA thiolase; *β*-ketothiolase; an enzyme that catalyses the formation of acyl-CoA and acetyl-CoA from CoA and 3-oxoacyl-CoA. This is the concluding reaction of each cycle of the fatty acid oxidation pathway (**beta oxidation**). Different enzymes exist in the mitochondrion and peroxisome, both being included in the **thiolase** family. Examples include rat peroxisomal enzyme A (one of two), homodimer: database code for precursor THI1_RAT, 424 amino acids (43.77 kDa); also from yeast (precursor): database code THIK_YEAST, 417 amino acids (44.68 kDa); mitochondrial enzyme, homotetramer: database code THIM_RAT, 397 amino acids (41.82 kDa).

acetyl-CoA carboxylase EC 6.4.1.2; *systematic name*: acetyl-CoA:carbon-dioxide ligase (ADP-forming); a multienzyme complex involved in the formation of **malonyl-CoA**, the first step in fatty-acid biosynthesis. It catalyses a reaction between ATP, acetyl-CoA, and HCO_3^- to form ADP, orthophosphate, and malonyl-CoA. Biotin is a cofactor. In bacteria it is a heterohexamer of biotin-carboxyl-carrier-protein, biotin carboxylase, and a 2:2 complex of the two subunits of carboxyl transferase. Examples from *Escherichia coli*: biotin carboxylase (EC 6.3.4.14), which catalyses the reaction between ATP, biotin-carboxyl-carrier-protein, and CO_2 to form ADP, orthophosphate, and carboxybiotin-carboxyl-carrier-protein; database code ACCC_ECOLI, 449 amino acids (49.26 kDa); biotin-carboxyl-carrier-protein: database code BCCP_ECOLI, 156 amino acids (16.67 kDa); carboxyl transferase α-subunit, database code ACCA_ECOLI, 318 amino acids (35.07 kDa); carboxyl transferase β-subunit, database code ACCD_ECOLI, 304 amino acids (33.31 kDa). Biotin-carboxyl-carrier-protein is carboxylated by biotin carboxylase and the carbonyl group is then transferred to acetyl-CoA by carboxyl transferase, thus forming malonyl-CoA. In mammals the activity is part of a trifunctional enzyme that has in a single protein the activities carboxyl carrier protein, biotin carboxylase (EC 6.3.4.14), and acetyl-CoA carboxylase (EC 6.4.1.2). Example from rat: database code COAC_RAT, 2345 amino acids (264.89 kDa).

[acetyl-CoA carboxylase] kinase EC 2.7.1.128; an enzyme that catalyses the phosphorylation by ATP of [acetyl-CoA carboxylase] with release of ADP. This phosphorylation step is one of the regulatory mechanisms for acetyl-CoA carboxylase, causing that enzyme to dissociate from an active polymeric form to an inactive monomeric form.

[acetyl-CoA carboxylase] phosphatase EC 3.1.3.44; an enzyme that catalyses the hydrolysis of phosphate from [acetyl-CoA carboxylase] phosphate. It reverses the phosphorylation catalysed by [acetyl-CoA carboxylase] kinase.

acetyl coenzyme A *abbr.*: acetyl-CoA; a derivative of **coenzyme A** in which the sulfhydryl group is acetylated. Originally termed 'active acetate', it is an important metabolite, derived from pathways such as glycolysis, fatty-acid oxidation, and degradative metabolism of some amino acids. It is further metabolized by the **tricarboxylic-acid cycle** and represents a key intermediate in lipid and terpenoid biosynthesis and other anabolic reactions.



***N*-acetylcysteine** *or* ***N*-acetyl-L-cysteine** a thiol-protecting agent used intravenously as an antidote in acetaminophen poisoning. It acts by enhancing glutathione synthesis, thereby increasing the capacity for detoxification and excretion of acetaminophen as a **mercapturic acid**. Methionine can be similarly used. It also has **mucolytic** properties, and is used in aiding the isolation of mycobacteria from sputum.

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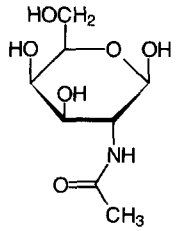
***N*-acetylgalactosamine** *symbol*: D-Gal*p*NAc; *abbr.*: NAGA; the D isomer, 2-acetamido-2-deoxy-D-galactopyranose, is a common structural unit of oligosaccharides, such as the blood-group substances and *O*-linked glycoproteins, in which the sugar is in glycosidic linkage to a protein or serine residue, or, in the case of the blood-group substances, to a lipid hydroxyl group. The reactant in synthetic reactions is UDP-*N*-acetylgalactosamine, which is formed by epimerization of *N*-acetylglucosamine.



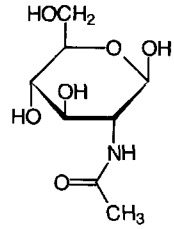
β-D-anomer

***N*-acetylgalactosamine-4-sulfatase** EC 3.1.6.12; *other names*: arylsulfatase B; chondroitinsulfatase; chondroitinase; an enzyme that hydrolyses the 4-sulfate groups of the *N*-acetyl-D-galactosamine 4-sulfate units of chondroitin sulfate and dermatan sulfate. It is a lysosomal enzyme involved in the degradation of proteoglycans, which accumulate in Maroteaux–Lamy syndrome (**mucopolysaccharidosis VI**), a storage disease resulting from a deficiency of the enzyme. Example (precursor) from human: database code ARSB_HUMAN, 533 amino acids (59.62 kDa).

***N*-acetylgalactosamine-6-sulfatase** EC 3.1.6.4; *other names*: chondroitinsulfatase; chondroitinase; galactose-6-sulfate sulfatase; an enzyme that hydrolyses the 6-sulfate groups of the *N*-acetyl-D-galactosamine 6-sulfate units of chondroitin sulfate, and also the D-galactose 6-sulfate units of keratan sulfate. It is a lysosomal enzyme involved in the degradation of proteoglycans. Keratan sulfate and chondroitin 6-sulfate accumulate in Morquio A syndrome, a storage disease resulting from a deficiency of the enzyme. Example (precursor) from human: database code GA6S_HUMAN, 522 amino acids (57.96 kDa).

***N*-acetylgalactosaminidase** EC 3.2.1.53; either of two types of enzyme that catalyse the hydrolysis of respectively *α*- and *β*-linked terminal nonreducing *N*-acetyl-D-galactosamine residues. Both are lysosomal enzymes. Deficiency of *α*-*N*-acetylgalactosaminidase is associated with a storage disease in which sialyloligosaccharides are found in urine.

***N*-acetylglucosamine** *symbol*: D-Glc*p*NAc; *abbr.*: NAG; the D isomer, 2-acetamido-2-deoxy-D-glucopyranose, is a common structural unit of plant glycoproteins and of many animal and bacterial glycoproteins. It is often the terminal sugar of an oligosaccharide moiety of a glycoprotein, linked glycosidically to the amide nitrogen of a protein asparagine residue. The acetyl group is introduced in a reaction between acetyl-CoA and glucosamine 6-phosphate to give *N*-acetylglucosamine 6-phosphate, which undergoes a mutase reaction to form *N*-acetylglucosamine 1-phosphate, from which UDP-*N*-acetylglucosamine is formed. The latter is the reactant in pathways of oligosaccharide synthesis and is also a precursor of *N*-acetylneuraminic acid (*see* **sialic acid**).



β-D-anomer

***N*-acetylglucosamine phosphotransferase** EC 2.7.1.69; *systematic name*: protein-N^{π}-phosphohistidine: sugar *N*-*pros*-phosphotransferase; *other name*: enzyme II of the phosphotransferase system; an enzyme that catalyses the reaction:

protein N^{π}-phosphohistidine + sugar = protein histidine + sugar phosphate.

It is a component of the phospho*enol*pyruvate-dependent sugar phosphotransferase system, a major carbohydrate active-transport system; the phosphoryl group from phospho*enol*pyruvate is transferred to phosphoryl carrier protein **HPR** by enzyme I, and from phospho-HPR to the sugar by enzyme II. It is an integral membrane protein. Example from *Escherichia coli*: database code PT2N_ECOLI, 648 amino acids (68.27 kDa).

***N*-acetylglucosamine-6-sulfatase** EC 3.1.6.14; an enzyme that catalyses the hydrolysis of sulfate groups of *N*-acetyl-D-glucosamine 6-sulfate units of heparan sulfate and keratan sulfate. It is a lysosomal glycoprotein. A deficiency is associated with the storage disease **mucopolysaccharidosis III**. Example (precursor) from human: database code GL6S_HUMAN, 552 amino acids (62.01 kDa).

***N*^{4}-(*β*-*N*-acetylglucosaminyl)-L-asparaginase** EC 3.5.1.26; *other names*: aspartylglucosylamine deaspartylase; aspartylglucosylaminase; glycosylasparaginase; an enzyme that catalyses the hydrolysis of N^4-(*β*-*N*-acetyl-D-glucosaminyl)-L-asparagine, released from glycoproteins, to *N*-acetyl-*β*-glucosaminylamine and L-aspartate. A deficiency of the enzyme results in the lysosomal storage disease, **aspartylglucosaminuria**, in which there is an accumulation of the enzyme's substrate. Example (precursor) from human: database code ASPG_HUMAN, 346 amino acids (37.15 kDa).

***N*-acetylglucosaminyl transferase** any of various glycosyltransferase enzymes within the subclass EC 2.4.1 that transfer an *N*-acetylglucosaminyl residue from UDP-*N*-acetyl-glucosamine to an oligosaccharide, and which are important in oligosaccharide synthesis. An example is EC 2.4.1.144, *β*-1,4-mannosyl-glycoprotein *β*-1,4-*N*-acetylglucosaminyltransferase; *other name*: *N*-glycosyl-oligosaccharide-glycoprotein *N*-acetylglucosaminyltransferase III. It catalyses the addition of *N*-acetylglucosamine in *β*(1-4) linkage to the *β*-linked mannose of the trimannosyl core of *N*-linked sugar chains. It is a type II membrane protein of the Golgi stack. Example from rat: database code GNT3_RAT, 536 amino acids (61.69 kDa). *See also* ***N*-acetyllactosamine synthase**, **lipopolysaccharide**, ***N*-acetylglucosaminyltransferase**, **UDP-*N*-acetylglucosamine-dolichyl phosphate-*N*-acetylglucosamine phosphotransferase**.

***β*^{6}-*N*-acetylglucosaminyltransferase** *see* **β-1,3-galactosyl-*O*-glycosyl-glycoprotein β-1,6-*N*-acetylglucosaminyltransferase**.

***N*-acetylglutamate synthase** (*abbr.* AGS) *see* **amino-acid *N*-acetyltransferase**.

acetylglutamic acid the L isomer, *N*-acetyl-L-glutamic acid, is a key intermediate in ornithine formation in bacteria and plants. It is converted to *N*-acetyl-L-glutamic *γ*-semialdehyde, from which *N*-acetyl-L-ornithine is formed in a transamination reaction. It activates **carbamoyl-phosphate synthase** (ammo-

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nia). It is formed from acetyl-CoA and glutamate by the action of amino acid *N*-acetyltransferase, EC 2.3.1.1.

β-*N*-acetylhexosaminidase EC 3.2.1.52; *other names*: β-hexosaminidase; hexosaminidase; an enzyme that catalyses the hydrolysis of terminal nonreducing *N*-acetyl-D-hexosamine residues in *N*-acetyl-β-D-hexosaminides. Example from human: database code HEXA_ HUMAN, 529 amino acids (60.62 kDa).

***N*-acetyllactosamine synthase** EC 2.4.1.90; *systematic name*: UDPgalactose:*N*-acetyl-D-glucosamine 4-β-D-galactosyltransferase; *other names*: *N*-acetylglucosamine β-(1→4)-galactosyltransferase; UDPgalactose-*N*-acetyl-glucosamine β-D-galactosyltransferase. An enzyme, located in the rough endoplasmic reticulum, that catalyses a reaction between UDPgalactose and *N*-acetyl-D-glucosamine to form UDP and *N*-acetyllactosamine. In humans the enzyme also has the activity of β-*N*-acetylglucosaminyl-glycopeptide β-1,4-galactosyltransferase (EC 2.4.1.38); *other names*: glycoprotein 4-β-galactosyltransferase; thyroid galactosyltransferase; UDPgalactose–glycoprotein galactosyltransferase. It catalyses a reaction between UDPgalactose and *N*-acetyl-β-D-glucosaminylglycopeptide to form UDP and β-D-galactosyl-1,4-*N*-acetyl-β-D-glucosaminylglycopeptide. **α-Lactalbumin** is an allosteric regulator and converts this activity to **lactose synthase**. Database code NALS_HUMAN, 400 amino acids (44.22 kDa).

***N*-acetylmuramoyl-L-alanine amidase** *see* **autolysin**.

***N*-acetylneuraminic acid** *see* **sialic acid**.

acetyloleoylglycerol *see* **oleoylacetylglycerol**.

acetylsalicylic acid *see* **aspirin**.

ACG **1** a codon in mRNA for L-threonine. **2** *abbr. for* acycloguanosine (*see* **acyclovir**).

Ach *symbol for* the arachidoyl (i.e. eicosanoyl) group.

Δ_2Ach *symbol for* the (*all-Z*)-eicosa-8,11-dienoyl group; *see* **eicosadienoic acid**.

Δ_3Ach *symbol for* the (*all-Z*)-eicosa-5,8,11-trienoyl group; *see* **eicosatrienoic acid**.

Δ_4Ach *symbol for* the arachidonoyl (i.e.(*all-Z*)-eicosa-5,8,11,14-tetraenoyl) group; *see* **arachidonoyl**.

ACh *abbr. for* acetylcholine.

Achaete–Scute complex *see* **AS-C protein**.

A chain **1** the shorter polypeptide chain of **insulin**, containing 21 amino-acid residues. **2** the heavy chain (H chain) of an **immunoglobulin**.

achatin-1 an endogenous neuroexcitatory tetrapeptide, Gly-D-Phe-Ala-Asp, isolated from the ganglia of the giant African snail, *Achatina fulica*: database code ACH1_ACHFU.

AChE *abbr. for* acetylcholinesterase.

achiral not **chiral**. —**achirality** *n.*

achlorhydria an inability to secrete gastric acid. It is a disorder, probably autoimmune, that is linked with pernicious anemia.

achromic point the point in time during the action of amylase on starch at which the reaction mixture no longer gives a colour with iodine, i.e. the reaction has proceeded to the point when the starch has all been degraded at least as far as **achröodextrins**.

achröodextrin any **dextrin** that is small enough not to give a colour with iodine.

acid **1** in the Brønsted–Lowry concept, a molecular species having a tendency to lose a hydron forming a conjugate base, e.g.

$$A \rightleftharpoons H^+ + B;$$

$$HCl \rightleftharpoons H^+ + Cl^-;$$

$$RCOOH \rightleftharpoons H^+ + RCOO^-;$$

$$RNH_3^+ \rightleftharpoons H^+ + RNH_2.$$

2 in the Lewis concept, a substance capable of accepting from a base an unshared pair of electrons, which then form a covalent chemical bond, e.g.

$$F_3B + :NH_3 \leftrightarrow F_3B^{-}{-}{}^{+}NH_3.$$

acid anhydride any compound formed by the elimination of the elements of water from the acidic groups of two acids, e.g. acetic anhydride (two acetic acid molecules) or acetyl phosphate (one molecule each of acetic and phosphoric acids).

acid–base balance term descriptive of the hydrogen-ion status of the blood, the mechanisms that regulate it, and the causes of its deviation from normal.

acid–base catalysis catalysis of a chemical reaction in which either an acid or a base mediates the formation of a reactive intermediate.

acid–base titration a **titration** in which either acid or base is added to a solution and the progress of the titration is followed by pH measurements, either electrometrically or with the use of pH indicators.

acid carboxypeptidase *see* **cysteine-type carboxypeptidase**.

acid dissociation constant *or* **acidity constant** *symbol*: K_a; the thermodynamic equilibrium constant for the dissociation of an **acid**. For a dilute solution of a weak acid, HA, dissociating in water according to the equilibrium:

$$HA + H_2O \rightleftharpoons H_3O^+ + A^-,$$

$$K_a = (a_{H_3O^+} \times a_{A^-})/a_{HA}$$

where *a* is the **activity** of the species designated by the subscripts. The activity of the water has been omitted from the equation since it may be taken as unity for a dilute aqueous solution. K_a is a measure of the strength of the acid, i.e. of its ability to donate hydrons to water. *Compare* **basic dissociation constant**. *See also* **pK**.

acid dye a **dye** containing an anionic acidic organic group that binds to and stains positively charged macromolecules.

acidemia *or (esp. Brit.)* **acidaemia** (*archaic*) a condition in which there is excessive acidity (i.e. increased hydrogen-ion concentration, lowered pH) of the blood. *Compare* **acidosis**, **alkalemia**.

acid-fast bacillus any bacterium able to resist decolorization by mineral acids after the application of specific basic aniline dyes; this property is possible due to the presence in these organisms of **mycolic acid**, together with a semipermeable membrane that allows the passage of the stain but not of the decolorizing acid.

acid β-glucosidase *see* **glucosylceramidase**.

acid hydrolase any **hydrolase** enzyme that is active in mildly acidic conditions (pH 5–6); often found in **lysosomes**.

acidic **1** of, relating to, containing, or characteristic of an **acid**. *Compare* **basic** (def. 1). **2** having an acid reaction in water; of or relating to an aqueous solution having a pH < 7.0. *Compare* **basic** (def. 2).

acidic amino acid any amino acid containing more potentially anionic groups than potentially cationic groups. All such amino acids have a net negative charge at neutral pH. Examples are aspartic and glutamic acids.

acid mucopolysaccharide any of a group of related heteropolysaccharides, found widely distributed in animal connective tissues, that contain *N*-acetylated hexosamine in its characteristic repeating disaccharide unit. They include chondroitin, **chondroitin sulfates**, **dermatan sulfates**, hyaluronic acid (*see* **hyaluronate**), and **keratan sulfates**.

acid number *or* **acid value** the mass, in milligrams, of potassium hydroxide required to neutralize the free fatty acid in one gram of fat; a measure of the mass of free acid in the sample.

acidophilic **1** staining readily with **acid dyes**. **2** (of organisms) preferring or thriving in a relatively acid environment.

acidosis a clinical condition in which excess acid or a base deficit tends to cause increased hydrogen-ion concentration (i.e. lowered pH) in the blood.

acidosome a non-lysosomal vesicle found in the ciliate proto-

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zoan *Paramecium*. The organelle is involved in acidification of digestive phagocytic particles through fusion.

acidotropic seeking an acid environment. The term is used e.g. in connection with Ser/Thr protein kinases that require Glu or Asp as part of the recognition site. The resulting Ser(P) or Thr(P) then acts as an acidic residue, extending the site with the result that further Ser or Thr residues are phosphorylated.

acid phosphatase *abbr. (in clinical biochemistry)*: ACP; EC 3.1.3.2; *systematic name*: orthophosphoric monoester phosphohydrolase (acid optimum); *other names*: alkaline phosphomonoesterase; phosphomonoesterase; glycerophosphatase; a lysosomal enzyme (except in red cells). It catalyses the hydrolysis of orthophosphoric monoester to an alcohol and orthophosphate. Zinc and magnesium are cofactors. It is present in high concentrations in the prostate gland, and is also present in red cells, platelets, bone, liver, and spleen. Its measurement in blood may be of use clinically in monitoring progress in cases where prostatic cancer has metastasized, but not where cancer is confined to the prostate, being elevated in only about 30% of cases. Normal range in human plasma 4–11 IU L^{-1}. Example: human lysosomal acid phosphatase precursor: database code PPAL_HUMAN, 423 amino acids (48.29 kDa).

acid proteinase *an older name for* enzymes of the sub-subclass **aspartic endopeptidase**, EC 3.4.23. It was suggested by their characteristic low optimum pH.

acid sphingomyelinase *see* **sphingomyelin phosphodiesterase**.

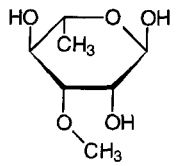
acinus (*pl.* **acini**) **1** a saclike structure that forms the terminal part of a gland. It comprises a cluster of cells surrounding a small duct. **2** one of the collection of small drupes making up an aggregate fruit such as a raspberry. —**acinar** *adj.*

ackee *or* **akee** a tree, *Blighia sapida*, native to tropical Africa and widely cultivated in the West Indies, especially Jamaica, for its fruit, the fleshy aril of which is edible when cooked and forms an important item of local diet. Unripe fruits contain toxic amounts of **hypoglycin** and can cause **Jamaican vomiting sickness**.

Acm *abbr. for* acetamidomethyl-.

AcNeu *(formerly) symbol for* *N*-acetylneuraminic acid (*see* **sialic acid**).

acofriose 6-deoxy-3-*O*-methylmannose; the L enantiomer is a component of some **cardiac glycosides**.



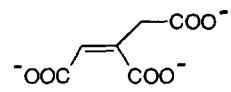
α-L-anomer

aconitase EC 4.2.1.3; *other name*: aconitate hydratase; *systematic name*: citrate (isocitrate) hydro-lyase. A hydrolase enzyme that catalyses the reaction:

$$\text{citrate} = \textit{cis}\text{-aconitate} + H_2O;$$

it also reversibly converts isocitrate into *cis*-aconitate + H_2O. An iron–sulfur protein, it removes H_R from the *pro-R*-CH_2–COOH group of citrate (*see* **citrate** for structure). Under kinetic conditions in which it forms isocitrate from citrate the product is (1*R*,2*S*)-1-hydroxypropane-1,2,3-tricarboxylate ((2*R*,3*S*)-isocitrate). Example from pig: database code NRL_5ACN, 754 amino acids (82.60 kDa); 3-D structure known.

aconitate the *cis* isomer, (*Z*)-prop-1-ene-1,2,3-tricarboxylate, is an intermediate in the conversion of citrate to isocitrate in the tricarboxylic-acid cycle, by the action of **aconitase**.



cis-aconitate

aconitate hydratase *see* **aconitase**.

aconitate Δ-isomerase EC 5.3.3.7; *systematic name*: aconitate Δ^2–Δ^3-isomerase. An enzyme that catalyses the reaction:

$$\textit{trans}\text{-aconitate} = \textit{cis}\text{-aconitate}.$$

acoustic gene transfer a method of transforming (typically plant) cells by using ultrasound.

ACP *abbr. for* **1** acyl carrier protein. **2** *(in clinical biochemistry)* acid phosphatase.

εAcp *(formerly) symbol for* a residue of the ε-amino acid ε-caproic acid, now known as 6-aminohexanoic acid. εAhx is the preferred symbol.

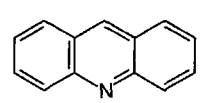
acquired immune deficiency syndrome *abbr.*: AIDS; defined by the Centers for Disease Control in the USA as a reliably diagnosed disease that is at least moderately indicative of an underlying immune deficiency or any other cause of reduced resistance reported to be associated with that disease. In humans it is a fatal condition (unless a successful therapy can be found), commonly associated with infection by **HIV**.

acquired immunity *or* **adaptive immunity** immunity (active or passive, humoral or cellular) that is established during the life of an individual, as contrasted with innate or natural immunity. Such immunity is specific for the inducing agent and is marked by an enhanced response on repeated encounters with that agent. The key features are memory (*see* **memory cell**) and specificity.

acquired tolerance **1** *(in immunology)* tolerance to an antigen that is established during the life of an individual. Immunological tolerance can (rarely) be produced in an adult animal by prolonged injection of massive doses of antigen. The tolerance persists as long as antigen persists in the animal. *See also* **self tolerance**. **2** *(in pharmacology)* tolerance (generally to psychoactive compounds) that develops on prolonged or repeated drug administration. It can be either **pharmacokinetic** usually by increased drug metabolism, or **pharmacodynamic**. *See* **tachyphylaxis, tolerance**.

acrasin a chemotactic substance produced by the myxamoebae of the cellular slime mould *Dictyostelium discoideum*, now identified as cyclic AMP.

acridine the parent compound of a series of derivatives e.g. 3,6-diaminoacridine (proflavin), that are potent mutagens. Some acridines are found in coal tar. They induce **frameshift mutations** during the replication of DNA by binding to DNA and distorting the double helix, causing additional bases to be incorporated or bases to be omitted. They are used as topical antiseptics and antimalarial agents.



Acridine Orange 3,6-bis(dimethylamino)acridine; a dye used as a probe of nucleic acids in microscopy and related techniques. When illuminated under UV light it yields a green (DNA) or reddish-orange (RNA) fluorescence.

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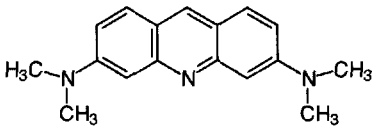

Acridine Orange

acriflavin a mixture of the **acridine** derivatives 3,6-diamino-10-methylacridinium chloride (about 65%) and **proflavin**.

acrocentric describing a chromosome in which the **centromere** is very close to one end.

acrolein 3-propenal; CH_2=CH–CHO; an unstable flammable liquid with a pungent odour that irritates the eyes and mucosae. It polymerizes (especially under light) to form a plastic solid.

acrolein test a qualitative test for the presence of glycerol, either free or esterified, based upon its oxidative dehydration to acrolein when heated with solid potassium hydrogen sulfate.

acromegaly a chronic disease marked by the gradual enlargement of the bones of the hands, feet, head, and chest with thickening of the skin, lips, and vocal chords. It is caused by excessive secretion of, or increased sensitivity to, **somatotropin**, and is often due to a tumour of the somatotrope cells of the pituitary.

acrosin EC 3.4.21.10; a trypsin-like serine endopeptidase. A major proteinase of mammalian spermatozoa, synthesized in a zymogen form, proacrosin, and stored in the **acrosome**. It comprises a heavy chain (catalytic) and a light chain linked by two disulfide bonds; it is not inhibited by α_1-antitrypsin. It catalyses the hydrolysis of Arg-|-Xaa and Lys-|-Xaa bonds, with preferential cleavage in the order Arg-|-Xaa >> Lys-|-Lys >> Lys-|-Xaa. Example (precursor) from human: database code ACRO_HUMAN, 421 amino acids (45.75 kDa).

acrosomal process a long thin actin-containing spike produced from the head of certain types of sperm when they make contact with the egg at fertilization. It is seen in sea urchins and other marine invertebrates having eggs surrounded by a thick gelatinous coat.

acrosome a structure in the head of a spermatozoon that contains acid hydrolases concerned in the breakdown of the outer membrane of the ovum during fertilization. It lies anterior to the nucleus just beneath the plasma membrane. *See also* **acrosin**.

acrylamide *or* **acrylamide monomer** *the trivial name for* propenamide, CH_2=CH–$CONH_2$; a water-soluble solid that is highly toxic and irritant, and readily polymerizes under the action of UV light or chemical catalysts into **polyacrylamide**.

ACTH *abbr. for* adrenocorticotrop(h)ic hormone (**corticotropin**).

1–24 ACTH *abbr. for* tetracosactrin.

actidione *see* **cycloheximide**.

actin a major protein constituent of the thin filaments of muscle and of the **microfilaments** found in practically all eukaryotic cells – it comprises 5–10% of the protein of such cells (*see* **actin filament**). In solutions of low ionic strength, actin is a globular 42 kDa monomer called **G-actin**. At physiological ionic strengths, G-actin polymerizes into a fibrous form called **F-actin**, which resembles two strings of beads wound round each other. F-actin is a helix of actin monomers with a helix diameter of about 7 nm, the structure repeating at intervals of 36 nm along the helix axis. When a solution of actin is mixed with a solution of the muscle protein myosin a complex called **actomyosin** is formed and the viscosity of the solution increases markedly. This increase in viscosity is reversed by the addition of ATP, which acts to dissociate the actomyosin complex. It is thought that the force of muscle contraction arises from an interaction of actin, myosin, and ATP. Example, α-cardiac actin (human): database code ACTC_HUMAN, 377 amino acids (41.97 kDa); seven motifs.

actin-binding domain a structural feature found in **actin-binding proteins**.

actin-binding protein any of several proteins that associate with either actin monomers or actin filaments in cells and modify their properties. Many of these proteins are found in the cell cortex, an actin-rich layer just below the plasma membrane. Examples include **dystropin**, **profilin**, **spectrin** and **ankyrin**, **fimbrin** and α-actinin (*see* **actinin**), **filamin**, **gelsolin**, and the **myosins**. The term is sometimes applied specifically to filamin.

actin depolymerizing factor *see* **destrin**.

actin filament a two-stranded helical polymer of the protein **actin**. Actin filaments form the thin filaments of muscle and also the **microfilaments** of the cytoskeleton of eukaryotic cells. Hence they are a major component of the contractile apparatus of skeletal muscle, and one of the three types of protein filament that form the cytoskeleton, the others being **microtubules** and **intermediate filaments**. The filaments, comprising polymerized globular actin molecules, appear as flexible structures with a diameter of 5–9 nm. They are organized into a variety of linear bundles, two-dimensional networks, and three-dimensional gels. In the cytoskeleton they are most highly concentrated in the cortex of the cell just beneath the plasma membrane.

actinic describing electromagnetic radiation, especially higher frequencies of visible light and UV radiation, capable of initiating photochemical reactions.

actinidine a monoterpenoid alkaloid occurring in *Actinidia polygama*.

actinin a minor protein constituent of muscle, found to be concentrated in both the Z line and the I band. Two components of actinin have been identified: **α-actinin**, F-actin cross-linking protein, is a dimer of ≈200 kDa with an action similar to that of **actinogelin**. Example from human: database code AACT_HUMAN, 892 amino acids (102.86 kDa); and **β-actinin**, a dimer of ≈70 kDa, is similar in action to **gelsolin**.

actinogelin a protein factor that effects Ca^{2+}-sensitive gelation of actin filaments. It was first obtained from Ehrlich ascites tumour cells, and has a molecular mass of 100–120 kDa. α-Actinin (*see* **actinin**) has a similar action.

actinoid *or* **actinide** any member of the series of 15 metallic elements with proton numbers 89 (actinium) to 103 (lawrencium) inclusive that occur together in group 3 and period 7 of the IUPAC **periodic table**; sometimes the term is restricted to the 14 elements following actinium. Actinoid is now the preferred name. All actinoids are radioactive, and those of proton number 93 or greater are artificial. They are all electropositive, and their chemical properties are similar, due usually to the filling of an inner electron subshell (5f) progressively across the series. Like the **lanthanoids**, they thus represent a series of inner transition elements.

actinomycin any of a large group of antibiotics isolated from various species of *Streptomyces* bacteria and characterized by having a substituted phenoxazine ring linked to two cyclic **heterodetic** peptides. The principal member of the group is **actinomycin D** (also called actinomycin C_1, actinomycin IV), which, at low concentrations, inhibits transcription without appreciably affecting DNA replication in both prokaryotic and eukaryotic cells. Actinomycin D binds tightly to duplex DNA thereby preventing it from being an effective template for RNA synthesis. Spectroscopic and hydrodynamic studies of complexes of actinomycin D and DNA suggest that the phenoxazine ring of actinomycin is intercalated between neighbouring base pairs in DNA. Other conformational studies indicate that actinomycin D recognizes the base sequence GpC in DNA.

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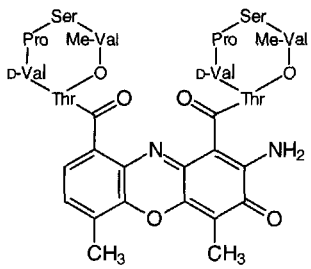

actinomycin D

actinomyosin *(formerly)* the contractile system in muscle comprising **actin** and **myosin**. *Compare* **actomyosin**.

action potential the localized change of electrical potential across a nerve fibre or muscle membrane that marks the position of an impulse as it is propagated. It is caused by sodium ion fluxes across the membrane resulting from transitory opening of **sodium channels**.

action spectrum a graph or table showing the relative efficiencies of different frequencies of radiation in causing a chemical or biochemical reaction, e.g. in photosynthesis or gas exchange. Efficiency, or **quantum yield**, is given by the measurable effect divided by the intensity of the (monochromatic) incident radiation.

activate **1** to make or render active, reactive, or capable of action. **2** to make radioactive. —**activated** *adj.*; **activation** *n.*

activated alumina particles of alumina, aluminium oxide, that have been rendered more adsorbent by heating strongly.

activated amino acid an amino-acid residue in an amino-acyladenylate molecule. The amino acid reacts with ATP to form aminoacyl-AMP in a reaction catalysed by an aminoacyl-tRNA synthetase. It is the first metabolic step in the biosynthesis of a polypeptide. The same enzyme catalyses the transfer of the amino acid to an ester link with the 3′-terminal hydroxyl of tRNA.

activated complex term that may be used to denote the assembly of atoms at the transition state of a chemical reaction.

activation **1** the action or process of rendering an atom, molecule, or other substance reactive or more reactive, whether physicochemically, chemically, or biochemically. **2** the process of rendering material artificially radioactive: radioactivation. *See* **radioactivation analysis**. **3** the initial changes in an ovum during fertilization, covering the period from first contact with a sperm to dissolution of the nuclear membranes. **4** the initial changes in the conversion of a spore to a vegetative cell. This can be effected by various agents or processes and may involve alteration of one of the spore's outer layers.

activation analysis *an alternative term for* **radioactivation analysis**.

activation energy *see* **Arrhenius equation**.

activation hormone a polypeptide hormone synthesized in the neurosecretory brain cells of insects. It regulates the functioning of the whole endocrine system, stimulating the secretory activity of other glands.

activator any substance that activates a chemical or enzymic reaction. The term was formerly used in biochemistry especially to describe metal-ion **cofactors** for enzymes.

activator constant *symbol*: K_A; the equilibrium **dissociation constant** of the reaction of an enzyme with an activator. For example, in the reaction:

$$E + A \rightleftharpoons EA,$$

$$K_A = [EA]/[E][A],$$

where [EA], [E], and [A] are the concentrations of enzyme–activator adduct, free enzyme, and free activator respectively.

active acetaldehyde *(sometimes)* the α-hydroxyethyl derivative, on C-2 of the thiazolidine ring, of thiamine diphosphate.

active acetate *(formerly) an alternative name for* **acetyl coenzyme A**.

active C_1 *abbr. for* active one-carbon.

active centre all the features of primary, tertiary, and quaternary structure of an enzyme – including the **active site** – that are required for substrate binding, specificity, and catalysis.

active-enzyme centrifugation a technique for determining the sedimentation and diffusion coefficients of an enzyme–substrate complex. A thin lamella of an enzyme solution is layered onto a substrate solution in an ultracentrifuge cell and, on rotation, as the enzyme molecules sediment in a band through the substrate solution they catalyse the enzymic reaction, the progress of which is observed optically (e.g. by spectrophotometry). The required coefficients are then calculated from either the rate of appearance of the product of the reaction or the rate of disappearance of the substrate. The centrifugation may be performed on impure enzyme preparations and at the very low concentrations of enzyme used in kinetic studies.

active fatty acid *(formerly) an alternative term for* an **acyl-CoA** derivative.

active formaldehyde *(formerly) an alternative term for* N^5,N^{10}-methylenetetrahydrofolate.

active immunity *or* **adaptive immunity** a type of immunity resulting from the stimulation of the immune response by an immunogen.

active immunization stimulation of the reactivity of the immune system of an individual towards an immunogen by administration of the immunogen, thereby producing a state of active immunity.

active methionine *or* **active methyl** *name sometimes used for* ***S*-adenosylmethionine**.

active methyl **1** *an alternative name for* **active methionine**. **2** one form of **active one-carbon** (e.g. 5-methyltetrahydrofolate).

active one-carbon any of the one-carbon units carried on tetrahydrofolate and concerned in a wide variety of biosynthetic reactions. They include the methyl-, methylene-, formimino-, formyl-, and methenyl- substituents.

active site **1** the general region of an enzyme molecule containing the **catalytic residues** identified with the binding and reaction of substrate(s). It includes those amino-acid residues that are, in the enzyme–substrate complex, either **contact amino acids**, i.e. those that at some point are only one bond distance removed from some point of the substrate molecule, or **auxiliary amino acids**, i.e. those that are not in such intimate physical contact with the substrate but nonetheless play a definite role in the action of the enzyme. *See also* **contributing amino acid**. **2** *(sometimes)* the portion of a peptide hormone responsible for its biological activity. Isolated fragments containing the active site may show some activity, but may function less efficiently than the intact hormone. *See also* **message sequence**.

active site-directed irreversible inhibitor a custom-made inhibitor of a given enzyme. Such inhibitors are typically trifunctional molecules containing: (1) a functional group able to bind to the enzyme's active site; (2) a nonpolar part that can interact with a nonpolar region on the enzyme, serving to align the inhibitor; and (3) an alkylating group capable of reacting with a susceptible group on the enzyme and irreversibly forming a covalent bond with it.

active sulfate *an alternative name for* **1 adenosine-5′-phosphosulfate**. **2 3′-phosphoadenosine-5′-phosphosulfate**.

active transport any energy-dependent process by which molecules or ions are transported across membranes against a chemical potential gradient. *Compare* **facilitated diffusion**, **simple diffusion**.

activin one of two gonadal glycoproteins related to **transforming growth factor-β** (the other is **inhibin**); present in two forms in

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human gonads, it exists as a dimer of inhibin β_A or β_B chains linked by disulfide bonds. Activin A is a dimer of β_A chains; activin AB is a dimer of β_A and β_B chains. A potent selective stimulator of FSH secretion by the anterior pituitary gland, not via GnRH receptors, it modulates induction of hemoglobin accumulation and proliferation of erythroid progenitor cells in human bone marrow culture and is important in embryonic axial development.

activity 1 the natural or normal functioning of an enzyme, hormone, inhibitor, or other agent; or the intensity with which such an agent functions. *See also* **enzymic activity**. 2 the number of nuclear **transformations** (def. 5) that occur or that can be detected in a given quantity of radioactive material in unit time (*see also* **becquerel**, **curie**). This term is also often used in this sense for **radioactivity** and, loosely, for the radioactive material itself or its emitted radiation; see also **specific activity**. 3 *or* **relative activity** *symbol*: a; the apparent or effective concentration of a chemical substance as judged by the behaviour of the substance in a standard state. The activity of an entity B is defined by

$$a_B = \exp[(\mu_B - \mu_B^o)/RT]$$

where μ_B and μ_B^o are respectively the chemical potential and standard chemical potential of entity B, R is the gas constant, and T the thermodynamic temperature. 4 **absolute activity** *symbol*: λ; the absolute activity of an entity B is defined by

$$\lambda_B = \exp(\mu_B/RT),$$

where μ_B is the chemical potential of entity B, R is the gas constant, and T is the thermodynamic temperature. *See also* **activity coefficient**.

activity coefficient *symbol*: γ; the ratio of the **activity** (def. 3) of a component of a solution to its concentration. When expressed on an amount concentration basis it is denoted γ_c, when on a molality basis γ_m, and when on a mole fraction basis γ_x. *See also* **mean ionic activity coefficient**.

activity stain any reagent that develops a colour when acted on by a particular enzyme. Such a reagent is used to detect the presence of an enzyme in a gel or paper electrophoresis strip, in which it differentially stains the enzyme protein in question but not other proteins.

actobindin a monomeric protein capable of binding two molecules of monomeric (i.e. G-) actin. Example from *Acanthamoeba castellanii*: database code ACTO_ACACA, 88 amino acids (9.53 kDa).

actomyosin *see* **actin**.

ACU a codon in mRNA for L-threonine.

acumentin an actin-modulating protein, Ca^{2+}-nondependent, isolated from rabbit alveolar macrophages.

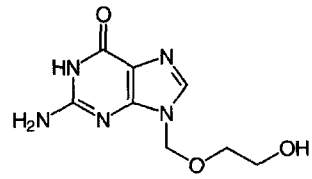
acute-phase protein any of the non-antibody proteins that show raised plasma concentrations soon after the onset of infection or tissue injury in homoiothermic animals. They include **complement** (def. 3) proteins, **C-reactive protein**, **fibrinogen** and other coagulation proteins, and **interferon**.

acute transfection the short-term infection of cells with DNA.

acyclic describing an organic compound devoid of a ring of atoms.

acycloguanosine *an alternative name for* **acyclovir**.

acyclovir *or* **acycloguanosine** 9-(2-hydroxyethoxymethyl)guanine; an antiviral agent widely used in the treatment of human herpes infections. It is selectively phosphorylated by herpesvirus-induced thymidine kinase and the phosphorylated compound is a potent inhibitor of herpesvirus-induced DNA polymerase. One proprietary name is Zovirax.



acyclovir

acyl *generic name for* any group formally derived by removal of a hydroxyl group from the acid function of an organic acid. Examples include any group of general structure R–CO– derived from a carboxylic acid; R–SO_2– from a sulfonic acid; and R–PO(OH)– from a phosphonic acid. However, unless the context indicates otherwise the term refers to such groups derived from carboxylic acids.

acyl-ACP dehydrogenase *see* **enoyl-[acyl-carrier protein] reductase (NADPH, A-specific)**.

acyl-activating enzyme *see* **long-chain-fatty-acid–CoA ligase**.

acylation the process of introducing an acyl group into a compound by substitution for a hydrogen atom. —**acylated** *adj.*

acyl carrier protein *abbr.*: ACP; any of the relatively small acidic proteins that are associated with the fatty acid synthase system of many organisms, from bacteria to plants. They contain one 4′-phosphopantetheine prosthetic group bound covalently by a phosphate ester bond to the hydroxyl group of a serine residue. The sulfhydryl group of the 4′-phosphopantetheine moiety serves as an anchor to which acyl intermediates are (thio)esterified during fatty-acid synthesis. In animals the fatty acid synthase system is a 500 kDa polyfunctional enzyme containing two identical chains, each with one ACP unit. *Escherichia coli* ACP, a separate single protein, contains 77 amino-acid residues (8.85 kDa); the phosphopantetheine group is linked to serine 36. Example (ACP-1 precursor) from *Arabidopsis thaliana*: database code ACP1_ARATH, 137 amino acids (15.04 kDa).

acyl-CoA *generic name for* any derivative of **coenzyme A** in which the sulfhydryl group is in thioester linkage with a fatty-acyl group.

acyl-CoA reductase EC 1.2.1.50; *recommended name*: long-chain-fatty-acyl-CoA reductase; *systematic name*: long-chain-aldehyde:$NADP^+$ oxidoreductase (acyl-CoA-forming). An enzyme that catalyses a reaction between a long-chain aldehyde, CoA, and $NADP^+$ to form long-chain acyl-CoA and NADPH. It is part of the bacterial **luciferase** system. Example: *see* **Lux proteins**.

acyl-CoA synthetase *see* **long-chain-fatty-acid–CoA ligase**.

acyl enzyme any intermediate formed in an enzymic acyltransfer reaction in which a group at the active site of the enzyme is acylated.

acylglycerol 1 any mono-, di-, or triester of glycerol with (one or more) fatty acids (termed respectively monoacylglycerol, diacylglycerol, or triacylglycerol); formerly known as mono-, di-, or triglyceride. 2 acylglycerols (*plural*), also denotes any mixture of mono-, di-, and/or triacylglycerols whatever its degree of complexity, including any comprising a **neutral fat**.

2-acylglycerol O-acyltransferase EC 2.3.1.22; *other names*: acylglycerol palmitoyltransferase; monoglyceride acyltransferase; an enzyme that catalyses the acylation by acyl-CoA of 2-acylglycerol to form diacylglycerol and CoA. It is an enzyme involved in the **monoacylglycerol pathway** of triacylglycerol biosynthesis.

1-acylglycerol-3-phosphate O-acyltransferase EC 2.3.1.51; *systematic name*: acyl-CoA:1-acyl-*sn*-glycerol-3-phosphate 2-*O*-acyltransferase. An enzyme that catalyses the acylation by acyl-CoA of 1-acyl-*sn*-glycerol 3-phosphate (lysophosphatidic acid) to form 1,2-diacyl-*sn*-glycerol 3-phos-

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phate (phosphatidic acid) with release of CoA. Acylated acyl carrier protein can also act as substrate. In animals, the enzyme specifically transfers unsaturated fatty acyl groups, a preference that contributes to the high proportion of unsaturated fatty acids on the 2-position of phosphoglycerides. Example from *Escherichia coli*: database code PLSC_ECOLI, 245 amino acids (27.42 kDa).

1-acylglycerophosphocholine *O*-acyltransferase EC 2.3.1.23; *other name*: lysolecithin acyltransferase; an enzyme that catalyses the acylation by acyl-CoA of 1-acyl-*sn*-glycero-3-phosphocholine to form 1,2-diacyl-*sn*-glycero-3-phosphocholine and CoA. It is involved in the resynthesis of phosphatidylcholine in situations where the latter has been degraded to lysophosphatidylcholine.

acylhomoserine *see* ***O*-succinylhomoserine**.

acyl migration any intramolecular rearrangement reaction in which, under certain conditions, an acyl group moves from one functional group to another, which may be of the same or of a different kind. **N → O acyl migration** (*also termed* N → O acyl shift, N → O acyl transfer, *or* N → O peptidyl shift) is a reaction that can occur in polypeptides and proteins subjected to hydrolysis by concentrated acid at room temperature or in the presence of an acid chloride (e.g. $POCl_3$), whereby the β-hydroxyl group of a serine or threonine residue displaces the amino group of the same residue from its amide (= peptide) linkage with the carboxyl group of the adjacent residue, thus forming an acid-sensitive β-ester linkage. The reaction may be used to advantage in partial acid hydrolysis of polypeptides and proteins. In the presence of alkali the ester reverts to the original amide by **O → N acyl migration**, a reaction that can also occur during the **Edman degradation** of a peptide. An acyl group, e.g. acetyl or maleyl, that happens to be present on the β-hydroxyl group of a serine or threonine residue, moves to the free amino group of such a residue when it becomes N-terminal, so preventing the next cycle of the degradation.

***N*-acylneuraminate glycohydrolase** *see* **sialidase**.

acylphosphatase EC 3.6.1.7; *systematic name*: acylphosphate phosphohydrolase. An enzyme that catalyses the hydrolysis of acyl phosphate to fatty-acid anion and orthophosphate. Example from chicken: database code ACYM_CHICK, 102 amino acids (11.27 kDa); three motifs.

acyl-protein synthase *see* **myelin-proteolipid *O*-palmitoyltransferase**.

acyl shift *see* **acyl migration**.

acylsphingosine deacylase *see* **ceramidase**.

***N*-acylsphingosine galactosyltransferase** EC 2.4.1.47; an enzyme that catalyses the formation of the cerebroside D-galactosylceramide from UDPgalactose and *N*-acylsphingosine with release of UDP.

acyltransferase any enzyme of sub-subclass EC 2.3.1. Such enzymes transfer acyl groups, forming either esters or amides, by catalysing reactions of the type:

acyl-carrier + reactant = acyl-reactant + carrier.

For example if acyl = acetyl, carrier = CoA, and reactant = choline, the reaction is that of **choline acetyltransferase**.

AD *(in clinical biochemistry) abbr. for* alcohol dehydrogenase (preferred to ADH because of possible confusion with antidiuretic hormone).

Ada *or* **ADA** *abbr. for N*-(2-acetamido)iminodiacetic acid; [(carbamoylmethyl)imino]diacetic acid; a **Good buffer substance**, pK_a (20 °C) = 6.6.

Adair equation an equation describing the oxygen saturation curve of hemoglobin:

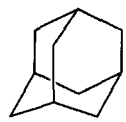
$$R = \frac{K_1[p_{O_2}] + 2K_1K_2[p_{O_2}]^2 + 3K_1K_2K_3[p_{O_2}]^3 + 4K_1K_2K_3K_4[p_{O_2}]^4}{4(1+K_1[p_{O_2}] + K_1K_2[p_{O_2}]^2 + K_1K_2K_3[p_{O_2}]^3 + K_1K_2K_3K_4[p_{O_2}]^4)}$$

where R is the fractional saturation of hemoglobin with oxygen, K_1, K_2, K_3, and K_4 are the stepwise intrinsic association constants for the four oxygen-binding sites, and p_{O_2} is the partial pressure of oxygen. For a generalized form of this equation *see* **Bjerrum formation function**. [Defined by Gilbert Smithson Adair (1896–1979), British biophysicist, in 1925.]

adamalysin EC 3.4.24.46; *other name*: proteinase II; a metalloendopeptidase that catalyses the cleavage of Phe^1-|-Val^2, His^5-|-Leu^6, His^{10}-|-Leu^{11}, Ala^{14}-|-Leu^{15}, Leu^{15}-|-Tyr^{16}, and Tyr^{16}-|-Leu^{17} in the insulin B-chain. Zn^{2+} and Ca^{2+} are cofactors. It is a snake venom proteinase whose natural substrate(s) are protease inhibitor(s), such as the **serpins**. Example from the Eastern diamondback rattlesnake, *Crotalus adamanteus*: database code ADAM_CROAD, 203 amino acids (23.05 kDa).

1-adamantanamine *or* ***α*-adamantanamine** *see* **amantadine**.

adamantane tricyclo[3.3.1.$1^{3,7}$]decane; a substance isolated from petroleum and said to have virostatic activity. *See also* **amantadine**.



adaptation *(in biology)* **1** any change in an organism's structure or function that allows it better to deal with its environmental conditions. **2** the mechanism whereby bacterial cells that approach cells of the opposite mating type, but fail to mate, can recover and continue dividing.

adapted gradient in **gradient elution**, a form of gradient in which the composition of the eluate is adjusted, on the basis of information obtained in a trial separation, to be optimal at each moment of the elution, so that the optimum resolution between the desired components of the sample is obtained.

adaptin a major coat protein of clathrin-coated vesicles. It functions as a component of the adaptor complexes that link clathrin to the receptors being taken into the cell in the coated vesicles, recognizing a motif of four amino acids (FRXY) in the cytoplasmic domain of the receptor. Example from rat: database code ADA5_RAT, 435 amino acids (49.60 kDa).

adaptive describing changes in an organism, induced by environmental factors, that tend to increase its viability.

adaptive enzyme *see* **inducible enzyme**.

adaptive immunity *an alternative name for* **active immunity**.

adaptor **1** any of various devices useful for joining together two or more parts, otherwise incompatible, such as electrical connectors or pieces of glassware. **2** any synthetic single- or double-stranded oligodeoxynucleotide useful in recombinant DNA technology for joining two incompatible cohesive ends of restriction fragments. *Compare* **linker**. **3** *or* **adaptor molecule** the molecule that was postulated as carrying the amino acid to the (messenger) RNA in the **adaptor hypothesis** of protein synthesis, now known to be a tRNA molecule.

adaptor hypothesis the hypothesis, first postulated by **Crick**, that during protein biosynthesis each amino-acid residue is carried to the RNA template by its appropriate small adaptor RNA molecule, and that the adaptor is the part that fits on to the messenger RNA. The hypothesis was subsequently confirmed by the discovery of **transfer RNA**.

ADCC *abbr. for* antibody-dependent cell-mediated cytotoxicity.

Addison's disease a disease due to deficiency of production of cortisol and other cortical steroids. It results from atrophy of the adrenal cortex, a condition having a variety of causes. [Described by Thomas Addison (1793–1860), British physician and endocrinologist, in 1849.]

addition **1** *(in chemistry)* the formation of an **adduct**. **2** an **addition reaction**.

addition compound *see* **adduct**.

addition reaction *or* **addition** any organic chemical reaction involving the combination of two or more substances to form a single product in which there are more groups attached to carbon atoms than there were in the original reactants. Such

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reactions thus involve a net reduction of bond multiplicity in one of the reactants, as in the example:

$$H_2C{=}CH_2 + Br_2 \rightarrow H_2BrC{-}CBrH_2.$$

address **1** that part of the information contained within the amino-acid sequence of a hormonal polypeptide or its biosynthetic precursors that determines the receptor-specific affinity of the hormone. *Compare* **message** (def. 4). **2** *(in computer technology)* a label, name, or number identifying a device or a location in a memory.

address sequence *or* **address region** that segment of the amino-acid sequence of a polypeptide hormone or prohormonal polypeptide in which the address of the hormone resides and through which the hormone is considered to bind to its specific receptor. *Compare* **message sequence**.

adducin a membrane skeleton protein (heterodimer) that interacts with a junctional complex that links **spectrin** assemblies. The complex in the red blood cell consists of **tropomyosin** and **actin** with band 4.1 (*see* **band**). Adducin probably binds to band 4.1. Examples from human erythrocyte: adducin α, database code S18207, 737 amino acids (80.88 kDa); adducin β, database code S18208, 726 amino acids (80.76 kDa).

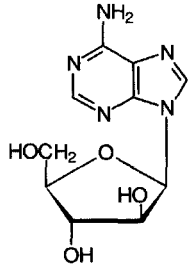
adduct **1** any new chemical species, AB, formed by direct combination of two separate chemical species, A and B, in such a way that there is no change in **connectivity** of atoms within the moieties A and B. This term is preferred to **complex**, which is less explicit. **2** *(formerly)* the product of a reaction between molecules occurring in such a way that the original molecules or their residues have their long axes parallel to one another.

Ade *symbol for* a residue of the purine base adenine (alternative to A).

ADE2 a gene that encodes a multifunctional protein with activities for **phosphoribosylaminoimidazole carboxylase** and **phosphoribosylaminoimidazolesuccinocarboxamide synthase**. It has been studied as a model of position effect in gene expression. The gene is expressed in all cells if in its normal position near the middle of the chromosome, but if moved experimentally to the end of the chromosome it is silenced. The lack of the enzyme produces a red pigmentation in these colonies.

adenine *symbol*: A *or* Ade; 6-aminopurine; 1*H*-purin-6-amine; a purine base. It is one of the five main bases found in nucleic acids and a component of numerous important derivatives of its corresponding ribonucleoside, adenosine. It can exist in a tautomeric imino form.

adenine arabinoside *other names*: vidarabine, ara-A; 9-β-D-arabinofuranosyladenine; an antibiotic produced by *Streptomyces* bacteria that acts as an antiviral agent, causing mispairing of purines and pyrimidines in nucleic-acid synthesis.



9-β-D-form

adenine nucleotide translocase *see* **ADP,ATP carrier protein**.

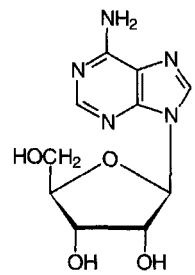
adenine phosphoribosyltransferase *abbr.*: APRT; EC 2.4.2.7; *other names*: AMP pyrophosphorylase; transphosphoribosidase; an enzyme that catalyses the formation of AMP from 5-phospho-α-D-ribose 1-diphosphate and adenine with release of pyrophosphate. It is an enzyme of purine metabolism that salvages adenine released by degradative enzymes, converting it back to a nucleotide. Example: from human: APT_HUMAN, 179 amino acids (19.45 kDa).

adeno+ *or (before a vowel)* **aden+** *comb. form* meaning of, pertaining to, or like a gland; glandular; found in glands.

adenohypophysis the glandular anterior lobe of the hypophysis (or **pituitary gland**). It produces corticotropin, gonadotropin, lipotropin, somatotropin, thyrotropin, and other hormones. *Compare* **neurohypophysis**. —**adenohypophyseal** *or* **adenohypophysial** *adj.*

adenoma any benign tumour formed by the multiplication of the epithelial cells that form the ducts and acini of glandular organs. The meaning has been broadened to include the benign tumours that arise from the solid masses of epithelium that form some of the endocrine glands. Adenomas often accurately reproduce the tissues from which they are derived and produce a secretion identical with or similar to that produced by the normal glandular tissue.

adenosine *symbol*: A *or* Ado; adenine riboside; 9-β-D-ribofuranosyladenine; a ribonucleoside found widely distributed in cells of every type as the free nucleoside and in combination in nucleic acids and various nucleoside coenzymes. It is a potent regulator of physiological transmission in both central and peripheral nervous systems, where it activates specific receptors (*see* **adenosine receptor**). It can inhibit or stimulate the release of a number of neurotransmitters, including acetylcholine, β-aminobutyrate, catecholamines, excitatory amino acids, and 5-hydroxytryptamine. The effect depends on whether the receptor involved inhibits adenylate cyclase (and thus inhibits release) or stimulates it.



adenosine aminohydrolase *see* **adenosine deaminase**.

adenosine 2′,3′-(cyclic)phosphate *see* **adenosine phosphate**.

adenosine 3′,5′-(cyclic)phosphate *see* **adenosine 3′,5′-phosphate**.

adenosine deaminase EC 3.5.4.4; *systematic name*: adenosine aminohydrolase; an enzyme that catalyses the hydrolysis of adenosine to inosine and NH_3. It is involved in the degradation of adenosine, the inosine thereby formed being then converted to hypoxanthine and thence to uric acid. The enzyme is also found on the outer surface of T cells, and a form that acts on double-stranded RNA (dsRNA) converts adenosines to inosines within dsRNA. Example from mouse, 3-D structure with 6-hydroxy-1,6-dihydropurine ribonucleoside: database code NRL_1ADA, 349 amino acids (39.62 kDa).

adenosine diphosphatase *see* **apyrase**.

adenosine 5′-diphosphate *symbol*: Ado5′*PP or* ppA; *the recommended name for* adenosine diphosphate (*abbr.*: ADP); 5′-diphosphoadenosine; 5′-adenylyl phosphate; adenosine 5′-trihydrogen diphosphate); a universally distributed nucleotide that occurs both in the free state and as a component

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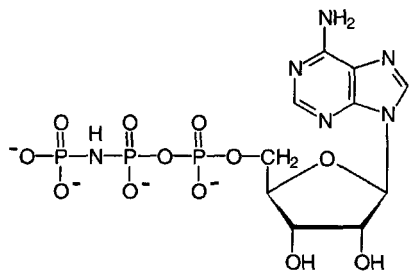
of certain **nucleotide coenzymes**. It is a metabolic precursor of adenosine 5′-triphosphate, ATP, and is the product of many enzyme reactions in which ATP is hydrolysed by an **adenosine triphosphatase** or in which the terminal phosphoric residue of ATP is transferred to another organic compound by a **kinase** (including **adenylate kinase**).

adenosinediphosphoglucose *or* **adenosine (5′)diphospho(1)-α-D-glucose** *symbol*: Ado*PP*Glc *or* Ado-5′*PP*-Glc *or* A5′pp1Glc; the alternative recommended names for adenosine diphosphate glucose (*abbr.*: ADPG or ADP-Glc or ADPglucose); adenosine 5′-(α-D-glucopuranosyl diphosphate); α-D-glucopyranosyl 5′-adenylyl phosphate; a **nucleoside-diphosphosugar** in which the distal phosphoric residue of adenosine 5′-diphosphate is in glycosidic linkage with glucose. ADPglucose is synthesized from glucose 1-phosphate and adenosine 5′-triphosphate, ATP, through the action of glucose 1-phosphate adenylyltransferase (EC 2.7.7.27). It is an intermediate in the incorporation of glucosyl groups into starch in plants and into storage glucans in bacteria.

adenosinediphosphoribose *or* **adenosine(5′)diphospho(5)-β-D-ribose** *symbol*: Ado*PP*Rib *or* A5′pp5Rib *or* (Rib5)ppA; *the alternative recommended names for* adenosine diphosphate ribose (abbr.: ADP-Rib *or* ADPribose); adenosine 5′-(β-D-ribofuranose 5-diphosphate); a **nucleoside diphosphosugar** in which the explicit sugar moiety is a second residue of D-ribose and is in ester linkage with the distal phosphoric residue of adenosine 5′-diphosphate atypically at C-5 instead of at C-1. ADP-ribose is synthesized from D-ribose 5-phosphate and ADP through the action of ribose-5-phosphate adenylyltransferase (EC 2.7.7.35), releasing orthophosphate. In addition, free ADP-ribose is released from nicotinamide-adenine dinucleotide, NAD^+, on hydrolytic cleavage of the glycosylamine bond to nicotinamide through the action of NAD^+ nucleosidase (EC 3.2.2.5). *See also* **cyclic adenosinediphosphoribose**.

adenosinediphosphoribosyl *abbr.*: ADPribosyl; the glycosyl group formally derivable from adenosinediphosphoribose by loss of the anomeric (i.e. C-1) hydroxyl group from its distal ribose moiety. The ADPribosyl group of nicotinamide-adenine dinucleotide may be utilized for **ADP-ribosylation**.

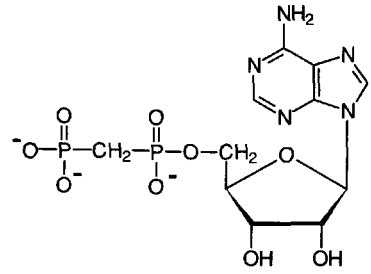
adenosine 5′-[β,γ-imido]triphosphate *symbol*: Ado*PP*[NH]*P* *or* p[NH]ppA; *the recommended name for* β,γ-imidoadenosine 5′-triphosphate (*abbr.*: ATP[β,γ-NH]); 5′-adenylyl imidodiphosphate; 5′-adenylyl iminodiphosphonate (*abbr.*: AMP-PNP); adenosine (5′→O^3)-1,2-μ-imidotriphosphate; a synthetic analogue of adenosine triphosphate, in which the oxy group between the latter's intermediate and terminal phosphorus atoms is replaced by an imido group. It competitively inhibits ATP-dependent enzymes, including mitochondrial ATPase.



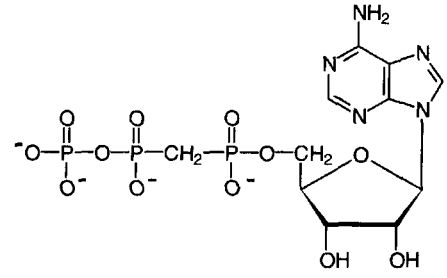
adenosine kinase EC 2.7.1.20; an enzyme that catalyses the reaction:

ATP + adenosine = ADP + AMP.

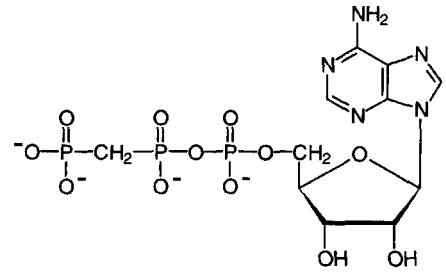
adenosine 5′-[α,β-methylene]diphosphate *symbol*: Ado*P*[CH_2]*P* *or* p[CH_2]pA; *the recommended name for* α,β-methyleneadenosine 5′-diphosphate (*abbr.*: ADP[α,β-CH_2]); 5′-adenylyl methylenephosphonate (*abbr.*: AMP-CP); adenosine (5′→O^1)-1,2-μ-methylenediphosphate; a synthetic analogue of adenosine 5′-diphosphate, ADP, in which the oxy group between the latter's two phosphorus atoms is replaced by a methylene group. It inhibits 5′-nucleotidase obtained from rat-heart membranes.



adenosine 5′-[α,β-methylene]triphosphate *symbol*: Ado*P*[CH_2]*PP* *or* pp[CH_2]pA; *the recommended name for* α,β-methyleneadenosine 5′-triphosphate (*abbr.*: ATP[α,β-CH_2]); 5′-adenylyl methylenediphosphate (*abbr.*: AMP-CPP); adenosine (5′→O^1)-1,2,-μ-methylenetriphosphate; a synthetic analogue of adenosine 5′-triphosphate, ATP, in which the oxy group between the latter's innermost and intermediate phosphorus atoms is replaced by a methylene group. It competitively inhibits rat-liver adenylate cyclase.



adenosine 5′-[β,γ-methylene]triphosphate *symbol*: Ado*PP*[CH_2]*P* *or* p[CH_2]ppA; *the recommended name for* β,γ-methyleneadenosine 5′-triphosphate (*abbr.*: ATP[β,γ-CH_2]); 5′-adenylyl methylenediphosphonate (*abbr.*: AMP-PCP); adenosine (5′→O^1)-1,2-μ-methylenetriphosphate; a synthetic analogue of adenosine 5′-triphosphate, ATP, in which the oxy group between the latter's intermediate and terminal phosphorus atoms is replaced by a methylene group. It inhibits the binding of ouabain to Na^+/K^+-transporting ATPase, the sodium pump.



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adenosine monophosphate *abbr.*: AMP; *an alternative name for* any **adenosine phosphate**, but in particular for adenosine 5′-phosphate, especially when its distinction from adenosine (5′-) diphosphate and adenosine (5′-)triphosphate requires emphasis.

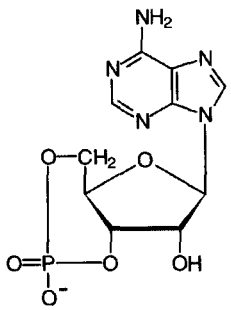
adenosine phosphate *symbol*: Ado*P*; adenosine monophosphate (*abbr.*: AMP); any phosphoric monoester or diester of adenosine. There are three monoesters – adenosine 2′-phosphate, adenosine 3′-phosphate, and **adenosine 5′-phosphate** – and two diesters – adenosine 2′,3′-phosphate and **adenosine 3′,5′-phosphate** – although adenosine 5′-phosphate is the ester commonly denoted (the locant being omitted if no ambiguity may arise). Adenosine 2′-phosphate (*symbol*: Ado2′*P*) is also named adenosine 2′-monophosphate (*abbr.*: 2′AMP) *or* 2′-adenylic acid *or* adenylic acid a, and adenosine 3′-phosphate (*symbol*: Ado3′*P*) is also named adenosine 3′-monophosphate (*abbr.*: 3′AMP) *or* 3′-adenylic acid *or* adenylic acid b *or* (*formerly*) yeast adenylic acid.

adenosine 2′-phosphate *see* **adenosine phosphate**.

adenosine 2′,3′-phosphate *see* **adenosine phosphate**.

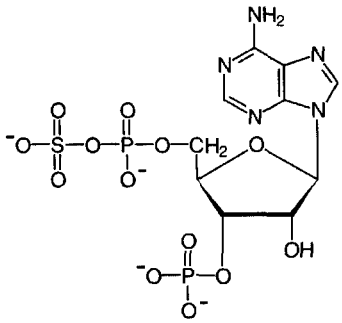
adenosine 3′-phosphate *see* **adenosine phosphate**.

adenosine 3′,5′-phosphate *symbol*: Ado-3′,5′-*P*; *the recommended name for* cyclic adenosine 3′,5′-monophosphate (*abbr.*: cyclic AMP *or* cAMP); adenosine 3′,5′-cyclophosphate; adenosine 3′,5′-(cyclic)phosphate; a monophosphoric diester of adenosine. It is a universally distributed key metabolite, produced by the action of **adenylate cyclase** on adenosine 5′-triphosphate, ATP. The first compound to be named a **second messenger**, it mediates many effects in signal transduction pathways. It was first identified as a heat-stable activator of glycogen phosphorylase kinase, and is now known also to activate cyclic-AMP-dependent protein kinase and to regulate numerous other enzymic activities or physiological processes.

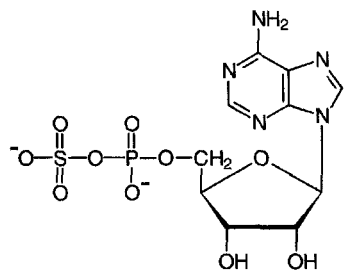


adenosine 5′-phosphate *or* **5′-adenylic acid** *or* **5′-phosphoadenosine** *or* **5′-*O*-phosphonoadenosine** *symbol*: Ado5′*P*; *alternative recommended names for* adenosine 5′-monophosphate (*abbr.*: 5′AMP); adenosine 5′-(dihydrogen phosphate); adenine (mono)ribonucleotide *or* (*formerly*) muscle adenylic acid. (The locant is commonly omitted if there is no ambiguity as to the position of phosphorylation.) It is a metabolic regulator, biosynthesized from inosine 5′-phosphate, 5′-inosinic acid; it is formed also by pyrophosphatase-catalysed cleavage of (inorganic) diphosphate from ATP.

adenosine 3′-phosphate 5′-phosphosulfate *or* **3′-phosphoadenosine 5′-phosphosulfate** *symbol*: *P*Ado*PS*; *abbr.*: PAPS; *alternative recommended names for* active sulfate; 3′-phospho-5′-adenylyl sulfate; adenosine 3′-phosphate 5′-*P*-phosphatosulfate; 3′-phospho-5′-adenylic sulfuric monoanhydride; a naturally occurring mixed anhydride. It is synthesized from **adenosine 5′-phosphosulfate** by phosphorylation with ATP through the action of adenylylsulfate kinase (EC 2.7.1.25). It is an intermediate in the formation of a variety of sulfo compounds in biological systems. For example, in animals it is involved in sulfate transfer in the formation of sulfatides and in the synthesis of chondroitin sulfate and other sulfated polysaccharides, while in bacteria, by a process analogous to that involving adenosine 5′-phosphosulfate in plants, adenosine 3′-phosphate 5′-phosphosulfate interacts with reduced thioredoxin to yield adenosine 3′,5′-bis(phosphate) and sulfite; the latter can then undergo further reduction to sulfide, from which cysteine may be synthesized.



adenosine 5′-phosphosulfate *symbol*: Ado*PS*; *abbr.*: APS; *the recommended name for* 5′-adenylyl sulfate; adenosine 5′-*P*-phosphatosulfate; 5′-adenylic sulfuric monoanhydride; a naturally occurring mixed anhydride. It is synthesized from ATP and (inorganic) sulfate by the action of sulfurylase, sulfate adenylyltransferase (EC 2.7.7.4), and is an intermediate in the formation of **adenosine 3′-phosphate 5′-phosphosulfate**. In plants, by a process analogous to that involving **adenosine 3′-phosphate 5′-phosphosulfate** in bacteria, adenosine 5′-phosphosulfate can undergo reduction to yield sulfide, which may then be utilized for cysteine synthesis.



adenosine receptor *or* **P_1 purinoceptor** one of three types, A_1, A_2, and A_3 of membrane protein that bind adenosine or its analogues; they are **seven-transmembrane-domain proteins**. The selective agonist for A_1 is N^6-cyclopentyladenosine; that for A_2 is (2-*p*-carboxyethyl)phenylamino-5′-*N*-carboxamidoadenosine. Binding of agonist to A_1 causes inhibition of **adenylate cyclase**, opening of K^+ channels, and inhibition of Ca^{2+} channels. Activation of A_2 brings about stimulation of adenylate cyclase. Activation of A_3 causes stimulation of adenylate cyclase. In some cases, particularly where A_1 receptors are involved, inositolphospholipid turnover may be stimulated. Examples (all from human): A_1 receptor: database code AAIR_HUMAN, 326 amino acids (36.15 kDa); A_2A receptor: database code AA2A_HUMAN, 412 amino acids (44.71 kDa); A_3 receptor: database code AA3R_HUMAN, 318 amino acids (36.18 kDa). *See also* **purinoceptor**.

adenosine 5′-β-thiodiphosphate *symbol*: Ado*PP*[S] *or* [S]ppA; *abbr.*: ADP[S] *or* ADP-β-S; *the recommended name for* adenosine 5′-[β-thio]diphosphate; adenosine 5′-(2-thiodiphosphate); adenosine $(5'\rightarrow O^2)$-1-thiodiphosphate; a synthetic

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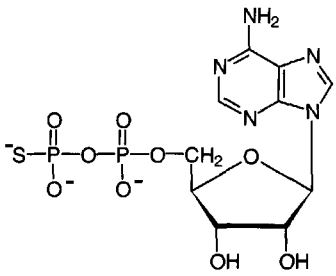
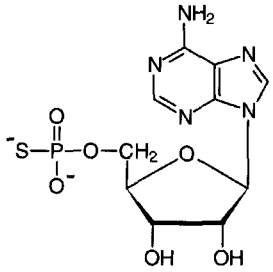
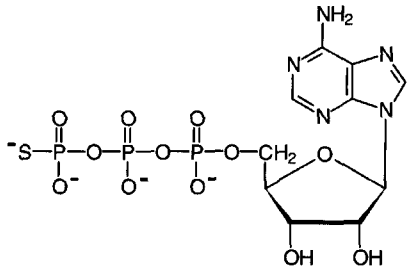
analogue of adenosine 5′-diphosphate, ADP, in which an oxygen atom of its terminal phosphoric residue is replaced by a sulfur atom. It acts variously as a substrate or an inhibitor of ADP-dependent systems.



adenosine 5′-thiophosphate *symbol*: Ado*P*[S] *or* [S]pA; *the recommended name for* adenosine 5′-[α-thio]monophosphate (*abbr.*: AMP-S); a synthetic analogue of adenosine 5′-phosphate, AMP, in which an oxygen atom of its phosphoric residue is replaced by a sulfur atom. It acts variously as a substrate or an inhibitor of AMP-dependent systems.

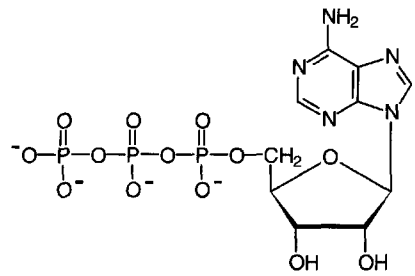


adenosine 5′-γ-thiotriphosphate *symbol*: Ado*PPP*[S] *or* [S]pppA; *abbr.*: ATP[S] *or* ATP-γ-S; *the recommended name for* adenosine 5′-[γ-thio]triphosphate; adenosine (5′→O^3)-1-thiotriphosphate; a synthetic analogue of adenosine 5′-triphosphate, ATP, in which an oxygen atom of its terminal phosphoric residue is replaced by a sulfur atom. It can variously substitute for ATP or act as an inhibitor of ATP-dependent systems.



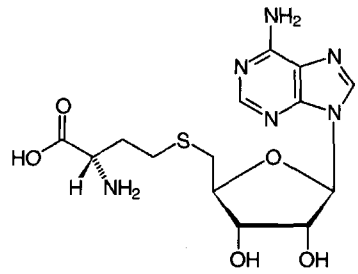
adenosinetriphosphatase *abbr.*: ATPase; **1** EC 3.6.1.3; ATP phosphohydrolase; an enzyme catalysing the hydrolysis of ATP to ADP and orthophosphate. **2** any of various enzymes listed separately as EC 3.6.1.32 to EC 3.6.1.38. Some function as exchangers or transporters for Na^+, K^+, or Ca^{2+} (*see* **calcium-transporting ATPase**, **sodium–potassium ATPase**); myosin ATPase (EC 3.6.1.32) is involved in muscle contraction; **H^+-transporting ATP synthase** (also called mitochondrial or chloroplast ATPase) (EC 3.6.1.34) is involved in ATP synthesis.

adenosine 5′-triphosphate *symbol*: Ado5′*PPP* or pppA; *the recommended name for* adenosine triphosphate (*abbr.*: ATP); 5′-triphosphoadenosine; 5′-adenylyl diphosphate; adenosine 5′-(tetrahydrogen triphosphate); a universally important coenzyme and enzyme regulator. It is formed from adenosine 5′-diphosphate by oxidative phosphorylation in coupled mitochondria, by photophosphorylation in plants, and by substrate-level phosphorylation. Reactions in which it participates are often driven in the direction leading to hydrolysis of ATP. The chemical energy so released may be utilized in active transport; it may be converted to mechanical energy (e.g. for muscular contraction, movement of cilia, etc.), to light energy (for bioluminescence), or to electrical energy (in electric fish); or it may be released as heat. ATP also participates in numerous synthetic reactions by the transfer to other metabolites of a phosphoric or a diphosphoric residue, of an adenosyl residue, or of an adenylyl residue.



adenosyl any chemical group formed by the loss of a 2′-, a 3′-, or a 5′-hydroxyl group from the ribose moiety of adenosine. *Compare* **adenylyl**.

S-adenosylhomocysteine the L enantiomer, *S*-(5′-adenosyl)-L-homocysteine (*symbol*: AdoHcy; *abbr.*: SAH), *S*-(5′-deoxyadenosine-5′-yl)-L-homocysteine, is formed from ***S*-adenosylmethionine**. It is a strong inhibitor of *S*-adenosylmethionine-mediated methylation reactions and is cleaved to adenosine and homocysteine.



***S*-adenosylmethionine** the L enantiomer, active methionine, *S*-(5′-adenosyl)-L-methionine (*symbol*: AdoMet; *abbr.*: SAM), *S*-(5′-deoxyadenosine-5′-yl)-L-methionine, is an important intermediate in one-carbon metabolism, the methionine's methyl group (activated by the adenosyl moiety bonded through sulfonium) being donated to an acceptor molecule by transmethylation and *S*-adenosylhomocysteine being produced. It is important also as an intermediate in the production of ethylene from L-methionine in plants, being cleaved to 5′-methylthioadenosine and 1-aminocyclopropane-1-carboxy-

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late. The latter compound is then fragmented under aerobic conditions to ethylene, formate, ammonium, and carbon dioxide.

adenosylmethionine decarboxylase EC 4.1.1.50; *systematic name*: *S*-adenosyl-L-methionine carboxy-lyase. An enzyme of polyamine (and hence **trypanothione**) biosynthesis that catalyses the decarboxylation of *S*-adenosyl-L-methionine to (5′-deoxyadenosin-5′-yl)(3-aminopropyl)methylsulfonium salt; pyruvate acts as a cofactor. The product participates in reactions in which its 3-aminopropyl group is transferred to **putrescine** to form **spermidine**, and a second 3-aminopropyl group is then transferred to spermidine to form **spermine**. In most cases its subunits (α and β) are derived from a single proenzyme. Example from yeast: database code DCAM_YEAST, 396 amino acids (46.18 kDa); α, 1–87; β, 88–end.

***S*-adenosylmethionine synthetase** *see* **methionine adenosyltransferase**.

adenovirus any of a group of non-enveloped icosahedral viruses, the Adenoviridae, containing linear double-stranded DNA. They affect mammals or birds (usually being specific to one or a few closely related host species) and are often associated with disease of the respiratory tract.

adenyl *a misnomer for* **adenylyl** or **adenylate**.

adenylate **1** either the monoanion or the dianion of adenylic acid. **2** any mixture of the acid and its anions. **3** any salt or ester of adenylic acid.

adenylate cyclase *or* **adenylylcyclase** *or (sometimes, incorrectly)* **adenyl cyclase** EC 4.6.1.1; *systematic name*: ATP pyrophosphate-lyase (cyclizing); a phosphorus–oxygen lyase enzyme that catalyses the elimination of a moiety of diphosphate from a molecule of adenosine 5′-triphosphate (ATP) to form **adenosine 3′,5′-phosphate** (cyclic AMP). It thereby is involved as an effector of signal transduction and other fundamental regulatory mechanisms. Its distribution is very wide, as also is its structural variation and the variation of its properties among the different forms. In mammals it is a membrane-bound glycoprotein, the various isoforms being in the mass range 115 to 180 kDa. They all have a predicted general structure indicating two structurally related cytoplasmic domains, relatively well conserved among the isoforms, having homology to the guanylate cyclase catalytic domain. One of them bears an ATP-binding site. In addition they have two membrane-spanning domains, each of which contains six membrane spans, the sequence differing significantly among the isoforms. Types I to VI have been described. Type I, 1134 amino acids, is brain-specific, Ca^{2+}/calmodulin activated, and inhibited by G-protein βγ subunits. Types II (1088 amino acids) and IV (1064 amino acids) are **calmodulin** insensitive and activated by βγ subunits; type II is found in brain and olfactory tissue, type IV is widely distributed except in testis. Type III, from olfactory sensory neurons, is calmodulin sensitive and not regulated by βγ subunits. Types V and VI form a subgroup that is widely distributed and not stimulated by βγ subunits. *Saccharomyces cerevisiae* enzyme (2026 amino acids) has a weak structural relationship with the mammalian enzyme. It is positively regulated by the *RAS1* and *RAS2* gene products, but this property is not shared by a recombinant enzyme from *Schizosaccharomyces pombe*. A plant gene has been cloned, the deduced protein sequence having no similarity to prokaryotic counterparts, but showing striking similarity to the catalytic region of *S. cerevisiae* adenylate cyclase, and with the cytoplasmic domains of bovine adenylate cyclase and two mammalian guanylate cyclases. Soluble adenylate cyclases are found in some bacterial toxins. Example from *Escherichia coli*: database code CYAA_ECOLI, 848 amino acids (97.43 kDa). Example from human: database code HSADCYCL, 476 amino acids (53.37 kDa).

adenylate energy charge (*or* **energy charge**) a measure of the phosphorylating power of an adenylate pool, equal to one half the average number of anhydride-bound phosphoric groups per adenosine moiety present in the pool. It may be defined in terms of the concentrations of AMP, ADP, and ATP in the pool and expressed by the quotient:

$$([ATP] + 0.5[ADP])/([ATP] + [ADP] + [AMP]).$$

Compare **phosphorylation state ratio**.

adenylate isopentenyltransferase EC 2.5.1.27; *other name*: cytokinin synthase; an enzyme that catalyses the reaction between Δ^2-isopentenyl diphosphate and AMP to form (N^6-Δ^2-isopentenyl)adenosine 5′-monophosphate, an intermediate in the formation of **zeatin** riboside, and pyrophosphate. Example from *Agrobacterium vitis* plasmid pTIS4: database code S30106, 236 amino acids (25.81 kDa).

adenylate kinase *abbr. (in clinical biochemistry)*: AK; EC 2.7.4.3; *systematic name*: ATP:AMP phosphotransferase; *other name*: myokinase. An enzyme that catalyses the reaction:

$$ATP + AMP = ADP + ADP.$$

Example, adenylate kinase isoenzyme 1 (human): database code KAD1_HUMAN, 194 amino acids (21.65 kDa), five motifs.

adenylate pool *or* **adenylate system** the total amount of AMP, ADP, and ATP in a cell, tissue, or organism.

adenyl cyclase *a misnomer for* **adenylate cyclase**.

adenylic acid *the trivial name for* any phosphoric monoester of adenosine. The position of the phosphoric residue on the ribose moiety of a given ester may be specified by a prefixed locant; *see* **adenosine phosphate**, **adenosine**. However, 5′-adenylic acid is the ester commonly denoted, its locant usually being omitted if no ambiguity may arise. 5′-Adenylic acid is also an alternative recommended name for **adenosine 5′-phosphate**.

adenylyl *the adenosine[mono]phospho group; the acyl group* derived from adenylic acid (*see* **adenosine 5′-monophosphate**). *Compare* **adenosyl**.

adenylylate to introduce adenylyl groups into a compound generally through the action of an adenylyltransferase. —**adenylylated** *adj.*; **adenylylation** *n.*

adenylyl cyclase *a misnomer for* **adenylate cyclase**.

adenylyl sulfate *see* **adenosine 5′-phosphosulfate**

adenylylsulfate kinase EC 2.7.1.25; *other name*: APS kinase; an enzyme that synthesizes 3′-phosphoadenosine-5′-phosphosulfate from ATP and adenylylsulfate with release of ADP. Example from yeast: KAPS_YEAST, 202 amino acids (23.03 kDa). See **phosphoadenosine-5′-phosphosulfate**.

adenylyltransferase *generic name for* any of a number of enzymes within sub-subclass EC 2.7.7, nucleotidyltransferases, that are specific for the transfer of an adenylyl group from a donor (usually adenosine triphosphate, ATP) to an acceptor (such as a nucleotide, a polynucleotide, a protein, a sugar phosphate, or sulfate); e.g. FMN adenylyltransferase (EC 2.7.7.2), ribose-5-phosphate adenylyltransferase (EC 2.7.7.35).

ADH *abbr. for*: **1** antidiuretic hormone. **2** *(in clinical biochemistry)* alcohol dehydrogenase (preferred form: AD).

adhalin *or* **DAG2** a dystrophin-associated glycoprotein of skeletal muscle sarcolemma that is specifically deficient in severe childhood autosomal recessive muscular dystrophy. It has a 17-residue signal sequence and one transmembrane domain, and there are two sites for N-linked glycosylation. Example from rabbit: database code OCDAGII, 387 amino acids (42.45 kDa).

adherens junction a **cell junction** in which the cytoplasmic face of the plasma membrane is attached to actin filaments.

adhesion *(in pathology)* the abnormal union of surfaces or parts, usually due to the formation of fibrous tissue following inflammation.

adhesion molecules molecules expressed on the surface of a cell that mediate the adhesion of the cell to other cells or to the extracellular matrix. They bind to receptors, classed collectively as **integrins**. Adhesion molecules are grouped into classes such as **selectins**; the immunoglobulin superfamily, which includes **ICAM**, **MadCAM**, **NCAM**, **PECAM**, and **VCAM**; the

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cadherins; and **CD44**. Adhesion molecules play a part in morphogenesis (e.g. cadherins) and in the treatment of inflammation and wounds (e.g. selectins and the immunoglobulin superfamily).

adiabatic describing any thermodynamic process that occurs with neither gain nor loss of heat between the system and its surroundings. —**adiabatically** *adv.*

adiabatic calorimeter a calorimeter in which the temperature of the outer jacket is kept as close as possible to that of the inner compartment so that heat losses from the latter are minimized.

adiabatic system *(in thermodynamics)* any geometrically defined volume that does not exchange thermal energy with its surroundings. *Compare* **closed system**, **open system**.

adipocyte a cell of adipose tissue; a fat cell or lipocyte of an animal.

adipogenesis the formation of fat or adipose tissue.

adipokinetic fat-mobilizing; lipotropic.

adipokinetic hormone *abbr.*: AKH; *an alternative name for* **lipotropin**.

adipose tissue fat or fatty tissue. *See also* **brown adipose tissue**, **white adipose tissue**.

adipsin **1** *another name for* complement factor D. **2** a protein of the serine endopeptidase family secreted into serum by adipocytes. It is expressed abundantly in adipocytes and sciatic nerve. There are two forms, of M_r 37 000 and 44 000.

adiuretin *(sometimes) an alternative name for* **antidiuretic hormone**.

adjuvant **1** *(in immunology)* any substance or mixture of substances that increases or diversifies the immune response to an antigen. *See also* **Freund's adjuvant**. **2** *(in pharmacology)* any remedy or drug that assists or modifies the action of other remedies or drugs.

adjuvant peptide *an alternative name for* **muramyl-dipeptide**.

ad lib without restraint. Short for the Latin *ad libitum*, meaning literally 'at pleasure'.

A-DNA *abbr. for* A-form of DNA.

Ado *symbol for* a residue of the ribonucleoside adenosine (alternative to A).

AdoHcy *symbol for S*-adenosylhomocysteine.

AdoMet *symbol for S*-adenosylmethionine.

adonitol *a former name for* **ribitol**.

adonose *a former name for* **ribulose**.

Ado*P* *symbol for* any adenosine phosphate.

Ado2′*P* *symbol for* adenosine 2′-phosphate.

Ado-2′,3′-*P* *symbol for* adenosine 2′,3′-phosphate.

Ado3′*P* *symbol for* adenosine 3′-phosphate.

Ado-3′,5′-*P* *symbol for* adenosine 3′,5′-phosphate.

Ado5′*P* *symbol for* adenosine 5′-diphosphate (alternative to **pAdo**).

Ado*P*[CH$_2$]*P* *symbol for* adenosine 5′-[α,β-methylene]diphosphate (alternative to p[CH$_2$]pA).

Ado*P*[CH$_2$]*PP* *symbol for* adenosine 5′-[α,β-methylene]triphosphate (alternative to pp[CH$_2$]pA).

Ado5′*PP* *symbol for* adenosine 5′-diphosphate (alternative to ppA).

Ado*PP*[CH$_2$]*P* *symbol for* adenosine 5′-[β,γ-methylene]triphosphate (alternative to p[CH$_2$]ppA).

Ado*PP*Glc *or* **Ado-5′*PP*-Glc** *symbol for* adenosinediphosphoglucose (alternatives to A5′pp1Glc).

Ado*PP*[NH]*P* *symbol for* adenosine 5′-[β,γ-imido]triphosphate (alternative to p[N]ppA).

Ado5′*PPP* *symbol for* adenosine 5′-triphosphate (alternative to pppA).

Ado*PP*[S] *symbol for* adenosine 5′-β-thiodiphosphate (alternative to [S]ppA).

Ado*P*[S] *symbol for* adenosine 5′-thiophosphate (alternative to [S]pA).

Ado*PPP*[S] *symbol for* adenosine 5′-γ-thiotriphosphate (alternative to [S]pppA).

Ado*PP*Rib *symbol for* adenosine diphosphoribose (alternative to A5′pp5Rib *or* (Rib5)ppA).

Ado*PS* *symbol for* adenosine 3′-phosphate 5′-phosphosulfate.

adoptive immunity immunity conferred by transfer of immunologically active cells from one individual to another.

ADP *abbr. for* adenosine 5′-diphosphate.

ADPase *abbr. for* adenosine diphosphatase (*see* **apyrase**).

ADP,ATP carrier protein *or* **adenine nucleotide translocase** an integral membrane protein of the inner mitochondrial membrane, responsible for the transport of ADP and ATP across the membrane. It exchanges one molecule of ADP^{3-} for one molecule of ATP^{4-}, and is thought to be driven by the proton gradient established across the inner membrane. It is a homodimer, each chain having three homologous domains. Different types occur in different mammalian tissues but all are related. Example, muscle isoform 1 (human): database code ADT1_HUMAN, 298 amino acids (33.03 kDa).

ADP[α,β-CH$_2$] *abbr. for* α,β-methyleneadenosine 5′-diphosphate; i.e. adenosine 5′-[α,β-methylene]diphosphate.

ADPG *abbr. for* adenosinediphosphoglucose; ADP-Glc is preferred.

ADP-Glc *or* **ADPglucose** *(preferred) abbr. for* adenosinediphosphoglucose; *see also* **ADPG**.

ADP-Rib *or* **ADPribose** *abbr. for* adenosinediphosphoribose.

ADP-ribose (cyclic) *see* **cyclic adenosine 5′-diphosphoribose**.

ADPribosyl *abbr. for* the adenosinediphosphoribosyl group.

ADP-ribosylation the transfer of one or more **adenosinediphosphoribosyl** (*abbr.* ADPribosyl) groups from nicotinamide-adenine dinucleotide, NAD^+, to a protein through the action of an **ADP-ribosyltransferase**. In eukaryotic cells the transfer occurs particularly to the α subunits of **G proteins**, and then is stimulated by treatment with certain bacterial toxins such as **cholera toxin** or **pertussis toxin**. Linear poly(ADPribosyl) attachments, which may consist of up to 50 ADPribose units, are found on nuclear proteins and also on some cytoplasmic proteins. In the stepwise generation of such attachments an incoming ADPribosyl group forms a (1′2′) glycosidic bond to the nucleosidic ribose moiety of the most recently attached ADP-ribose unit. ADP-ribosylation occurs also in cells of *Escherichia coli* infected with bacteriophage T4, where single ADPribosyl groups become attached to the host's RNA polymerase. —**ADP-ribosylated** *adj. See also* **ADP-ribosyltransferase**, **NAD(P)$^+$–arginine ADP-ribosyltransferase**.

ADP-ribosylation factor a protein that acts as activator for **ADP-ribosyltransferase**. Example (human and bovine): **cholera toxin** activator: database code ARF1_HUMAN, 181 amino acids (20.67 kDa).

ADP-ribosyltransferase EC 2.4.2.30; *recommended name*: NAD^+ ADP-ribosyltransferase; *systematic name*: NAD^+: poly(adenine-diphosphate-D-ribosyl)-acceptor ADP-D-ribosyl-transferase; *other names*: poly(ADP) polymerase; poly(adenosine diphosphate ribose) polymerase; NAD^+ ADP-ribosyltransferase (polymerizing); poly(ADP-ribose) synthetase; *abbr.*: PARP *or* ADPRT. An enzyme that catalyses a reaction between NAD^+ and (ADP-D-ribosyl)$_n$-acceptor to form nicotinamide and (ADP-D-ribosyl)$_{n+1}$-acceptor. The enzyme acts on a number of nuclear proteins and thereby regulates events in differentiation and cell proliferation. The presence of DNA is necessary, and zinc is a cofactor. Example from *Bos taurus*: database code PPOL_BOVIN, 1015 amino acids (113.36 kDa).

ADP[S] *or* **ADP-β-S** *abbr. for* adenosine 5′-β-thiodiphosphate.

adren+ *or* **adreno+** *comb. form* denoting **1** the **adrenal gland(s)**. **2** **epinephrine** or a related catecholamine.

adrenal **1** pertaining to or produced by the **adrenal glands**. **2** the adrenal gland itself.

adrenal androgen any of the C_{19} steroid hormones produced in the cortex of the adrenal gland, including androstenedione and testosterone.

adrenal cortex *see* **adrenal gland**.

adrenal cortical hormone *or* **adrenocortical hormone** any (cor-

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tico)steroid hormone elaborated and secreted by the cortex of the **adrenal gland**.

adrenalectomize *or* **adrenalectomise** to carry out adrenalectomy. —**adrenalectomized** *or* **adrenalectomised** *adj.*

adrenalectomy surgical removal of one or (usually) both adrenal glands.

adrenal gland *or* (less commonly) **suprarenal gland** an endocrine organ in vertebrates. There is a single pair in mammals, one near each kidney; in other vertebrates there may be multiple adrenal glands. The gland has two components: an inner medulla, derived from the neural crest, that biosynthesizes and secretes epinephrine and norepinephrine; and an outer cortex, derived from the coelom, that is concerned in the biosynthesis and secretion of steroid hormones. The cortex consists in turn of three histologically defined zones: an outer **zona glomerulosa**, the cells of which are responsible for the biosynthesis of aldosterone and deoxycorticosterone; an intermediate **zona fasciculata**; and an inner **zona reticularis**. The cells of the zona fasciculata and zona reticularis are responsible for the biosynthesis of the glucocorticoid cortisol and the androgens dehydroepiandrosterone and androstenedione.

adrenaline *see* **epinephrine**.

adrenal medulla *see* **adrenal gland**.

adrenal medullary hormone any catecholamine hormone elaborated and secreted by the adrenal medulla. *See* **adrenal gland**.

adrenergic **1** describing a nerve or other cell, or cell receptor (*see* **adrenoceptor**) that is activated by epinephrine, norepinephrine, or an epinephrine-like substance. **2** any nerve that acts by releasing epinephrine, norepinephrine, or an epinephrine-like substance from its nerve ending. *See also* **cholinergic**, **GABAergic**, **noradrenergic**, **peptidergic**, **purinergic**, **serotonergic**. —**adrenergically** *adv.*

adrenergic receptor *an alternative term for* **adrenoceptor**.

β-adrenergic-receptor kinase *abbr.*: βARK, βAR kinase *or* BARK; EC 2.7.1.126; an enzyme that phosphorylates specifically only the agonist-occupied form of the β-adrenoceptor and closely related receptors at the C terminus. It appears to be important in mediating rapid agonist-specific (homologous) desensitization. Its cDNA codes for a precursor protein of 689 amino acids, database code ARK1_HUMAN (79.58 kDa). The purified protein migrates as a single band of 80 kDa on electrophoresis. It has a protein kinase catalytic domain that has sequence similarity to protein kinase C and cyclic AMP-dependent protein kinase.

adrenic acid *see* **docosatetraenoic acid**

adreno+ *see* **adren+**.

adrenoceptor *or* **adrenergic receptor** *or* **adrenoreceptor** *or* **adrenotropic receptor** any receptor on an effector cell that is activated by epinephrine or related catecholamines. Structurally they are all of the seven-transmembrane-domain type. Adrenoceptors may be classified phenomenologically into different types according to their sensitivities to agonists and antagonists.

α Adrenoceptors have a relative order of agonist potency: epinephrine ≥ norepinephrine > isoprenaline (isoproterenol), and a relative order of antagonist potency: phentolamine >> propranolol. They are associated with stimulatory effects such as vasoconstriction and contraction of the iris, nictitating membrane, urinary bladder, seminal vesicles, and vas deferens and with relaxation of propulsive smooth muscle in the gut. In some species they mediate stimulation of gluconeogenesis and hepatic glycogenolysis. There are two groups, α_1 and α_2. α_1 Receptors act through the phosphoinositide/Ca^{2+} second messenger system and are of four subtypes: α_{1A}, norepinephrine > epinephrine, 560 amino acids (rat); α_{1B}, norepinephrine = epinephrine, 515 amino acids (rat); α_{1C}, norepinephrine = epinephrine (different antagonist sensitivity from α_{1B}), 466 amino acids (bovine); α_{1D}, 560 amino acids (rat). α_{2A} Receptors all inhibit the formation of cyclic AMP; they also open K^+ channels and inhibit Ca^{2+} channels; 450 amino acids (human). α_{2B} Receptors inhibit Ca^{2+} channels; 450 amino acids (human). α_{2C} Receptors have no effect on ion channels; 461 amino acids (human). Examples: α_{1A} receptor, database code AIAA_HUMAN, 572 amino acids (60.46 kDa); α_{2A} receptor (subtype c10), database code A2AA_HUMAN, 450 amino acids (48.96 kDa).

β Adrenoceptors have actions that can be ascribed to the activation of adenylate cyclase. They may be divided phenomenologically into three classes: (1) β_1 adrenoceptors, in which the relative order of agonist potency is isoprenaline > norepinephrine ≥ epinephrine and the relative order of antagonist potency is practolol > propranolol. They are associated with cardiac stimulation and glycogenolysis, lipolysis in white adipose tissue, and calorigenesis in brown adipose tissue; (2) β_2 adrenoceptors, in which the relative order of agonist potency is isoprenaline > epinephrine > norepinephrine and the relative order of antagonist potency is propranolol > practolol; they are associated with skeletal muscle glycogenolysis, promotion of secretion of glucagon and insulin, vasodepression, and bronchodilation; and (3) β_3 adrenoceptors with agonist potency norepinephrine > epinephrine. Examples from human: β_1, database code B1AR_HUMAN, 477 amino acids (51.16 kDa); β_2, database code B2AR_HUMAN, 413 amino acids (46.50 kDa); β_3, database code B3AR_HUMAN, 408 amino acids (43.47 kDa). *See also* **β-adrenergic receptor kinase**, **β-arrestin**.

adrenoceptor kinase *see* **β-adrenergic receptor kinase**.

adrenocortical of, pertaining to, or derived from the cortex of the **adrenal gland**, e.g. adrenocortical hormone. *See* **adrenal androgen**, **corticosteroid**.

adrenocorticotropic hormone *or* **adrenocorticotrophic hormone** *abbr.*: ACTH; *an alternative name for* **corticotropin**.

adrenocorticotropic hormone-releasing factor *an alternative name for* **corticotropin releasing hormone**.

adrenocorticotropin *or* **adrenocorticotrophin** *an alternative name for* **corticotropin**.

adrenodoxin *or (sometimes)* **adrenoredoxin** a **ferredoxin** isolated from adrenal-cortex mitochondria that acts as an electron carrier in hydroxylase systems acting on steroids. It transfers electrons from adrenodoxin reductase to **cholesterol monooxygenase**. Example from *Bos taurus*: database code ADX1_BOVIN, 186 amino acids (19.76 kDa); residues 1–58 are the mitochondrial transit sequence, 59–186 adrenodoxin. *See also* **NADPH:adrenodoxin oxidoreductase precursor**. *Compare* **putidaredoxin**.

adrenodoxin reductase *see* **NADPH:adrenodoxin oxidoreductase precursor**.

adrenomedullary of, pertaining to, or derived from the medulla of the **adrenal gland**.

adrenomedullin a hypotensive peptide that may function as a hormone in circulation control. Example from human: database code ADML_HUMAN, 185 amino acids (20.40 kDa).

adrenoreceptor *a variant spelling of* **adrenoceptor**.

adrenoredoxin *(sometimes) a variant spelling of* **adrenodoxin**.

adrenosterone androst-4-ene-3,11,17-trione; a hormone with weak androgenic effect, originally called Reichstein's substance G.

adrenotropic receptor *an alternative name for* **adrenoceptor**.

adrex *or* **adx** *abbr. for* adrenalectomized.

adriamycin *former (generic) name for* **doxorubicin**.

adseverin *another name for* **scinderin**.

adsorb to undergo or elicit **adsorption**. —**adsorbable** *adj.*; **adsorbability** *n.*

adsorbate a substance that is adsorbed to the surface of another substance from either a gas or a liquid phase.

adsorbent **1** capable of **adsorption**. **2** a solid that adsorbs another substance from either a gas phase or a liquid phase.

adsorptiochromism the colour change that sometimes ac-

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companies adsorption of organic compounds onto inorganic substances, e.g. onto alumina.

adsorption **1** any process in which a gas, liquid, or solute adheres to the exposed surfaces of a material, especially a solid, with which it is in contact. In **physical adsorption** the adhesion is through van der Waals forces of interaction, whereas in **chemisorption** (*or* chemical absorption) the adhesion is through formation of weak chemical bonds. *Compare* **absorption**. **2** *(in immunology)* the nonspecific attachment of an antigen (or antibody) onto the surfaces of red cells or inert particles so that the antibody (or antigen) to it may be detected by agglutination of the cells or particles. *Compare* **immunosorption**. **3** *(in microbiology)* the process of attachment of a phage or other virus to a cell.

adsorption chromatography any form of **chromatography** in which separation of the components of a mixture is based mainly on differences between the adsorption affinities of the components for the surface of an active solid.

adsorption coefficient in any adsorption equilibrium (of a substance from a solution), the mass of adsorbed substance per unit mass of adsorbent divided by the concentration of the substance in solution. It has the dimensions of reciprocal concentration. *Compare* **distribution coefficient**, **partition coefficient**.

adsorption isotherm any plot of the amount of solute adsorbed by an adsorbent (or of ligand bound by, e.g., a macromolecule, often expressed as the **saturation fraction**) versus the concentration of the free solute (or ligand), at constant temperature. *Compare* **Langmuir adsorption isotherm**.

adx *see* **adrex**.

AEBSF *abbr. for* aminoethylbenzenesulfonyl fluoride.

+aemia *see* **+emia**.

aequorin a Ca^{2+}-dependent **photoprotein** responsible for luminescence by oxidation of the chromophore coelenterazine. It is obtainable from the hydrozoan jellyfish *Aequorea forskaolea*. In the absence of any other cofactors or oxygen it emits light on the addition of calcium ions, making it useful for the determination of free calcium ions. Example, aequorin I from *Aequorea victoria*: database code AEQ1_AEQVI, 196 amino acids (22.49 kDa).

aerate **1** to supply with or expose to air. **2** to pass air through a liquid. —**aeration** *n.*

aerobe any organism or class of organisms that can grow in the presence of dioxygen. **Facultative aerobes** are also capable of growing in the absence of dioxygen, whereas **obligate** (or strict) **aerobes** have an absolute requirement for dioxygen. *Compare* **anaerobe**.

aerobic **1** describing conditions in which gaseous or dissolved dioxygen is present. **2** describing an organism or process that requires or is able to use dioxygen. **3** of or produced by an aerobe. *Compare* **anaerobic**.

aerolysin a channel-forming protein secreted by the human pathogen *Aeromonas hydrophila*. The cytolytic toxin is a dimer but forms stable heptameric structures that insert into lipid bilayers to produce well-defined channels, leading to destruction of the membrane permeability barrier and osmotic lysis. Example (precursor) from *A. hydrophila*: database code AERA_AERHY, 493 amino acids (54.28 kDa).

aerosol a colloidal dispersion of solid particles or liquid droplets in air or another gas.

Aet *symbol for* the aminoethyl group, $-CH_2-CH_2-NH_2$.

aetiology *see* **etiology**.

afamin a mammalian serum protein similar to albumin, α-fetoprotein, and vitamin D-binding protein. Example from human: database code HUMAFAMIN, 599 amino acids (68.99 kDa).

afferent **1** conveying inwards to a part, organ, or centre, as of a blood vessel, nerve, or duct. **2** an afferent part, e.g. an afferent blood vessel or afferent nerve. *Compare* **efferent**.

affine the quality of having affinity.

affinity **1** chemical attraction; the tendency of a chemical substance to combine with, bind to, or dissolve in other chemical substances. **2** any measure of such chemical attraction. **3** denoting biomolecular interaction that exhibits specificity.

affinity adsorbent any biospecific adsorbent used in affinity chromatography.

affinity chromatography a general chromatographic method that may, in principle, be used to isolate either of the components of a reversibly reacting chemical system provided that one component can be coupled to an insoluble matrix through a covalent linkage. The other component can then be bound to the immobilized component and the system eluted with a buffer that liberates the bound component. The technique has been applied to the separation of various substances, including enzymes, substrates, antigens, antibodies, nucleic acids, and even whole living cells. Pure antibodies can be prepared by this means: the antigen is covalently coupled to the dextran beads in the chromatography column, the antibody-containing solution is run into the column in neutral buffer, the specific antibody binds to the antigen, and the antibody is subsequently released with a buffer of high or low pH or with a denaturing reagent. The technique can also be used to isolate antigen. *See also* **affinity-elution chromatography**, **dye-ligand chromatography**. —**affinity-chromatographic** *adj.*

affinity constant *or* **binding constant** *an alternative name for* **association constant** (especially in relation to the binding of and/or to macromolecules, as in antigen–antibody, hormone–receptor, and enzyme–inhibitor reactions).

affinity cytochemistry a technique for detecting the distribution of specific cell-surface receptors. An easily visible (or electron-dense) material conjugated with a reagent specific for a particular cell-surface receptor is allowed to react with the cells in question and is then detected by light or electron microscopy.

affinity electrode a type of electrode useful for assaying specific proteins. It comprises a metal (e.g. titanium) wire whose surface has been oxidized and then covalently attached to a ligand capable of interacting biospecifically and reversibly with the protein in question. Binding of the complementary protein to the electrode results in a measurable change in electric potential relative to that given by a reference electrode. The latter is prepared in a similar way but lacks the specific ligand.

affinity electrophoresis *or* **affinoelectrophoresis** a type of **electrophoresis** in which the support medium contains an agent, immobilized by entrapment or by covalent linkage, that interacts specifically and selectively with certain of the components of the mixture to be analysed, thereby altering the electrophoretic mobility of those components.

affinity-elution chromatography a technique in which a compound that is nonspecifically bound to the matrix of a chromatographic column is specifically eluted by binding to a ligand in the eluting solvent. **Biospecific-elution chromatography** is a variant of this technique.

affinity gel any gel that serves as an **affinity matrix**.

affinity-isolated *an alternative term for* **affinity-purified**.

affinity label an active-site-directed irreversible inhibitor of an enzyme, antibody, or other protein. It is a chemically reactive compound that resembles a substrate or other specific ligand and bonds covalently to the active site or specific site on the protein. The affinity labelled groups can then be identified by **fingerprinting** and thus reveal the composition at the active site. It is sometimes termed **Trojan horse inhibitor**.

affinity matrix *or* **affinity support** any supporting material to which the biospecific reagent is attached in **affinity chromatography**.

affinity precipitation the precipitation of an enzyme by a homo- or hetero-bifunctional derivative of its coenzyme or/and a substrate or inhibitor. An example is the precipitation of **lactate dehydrogenase** by $N^{2\prime}$-adipodihydrazido-bis-(N^6-carbonylmethyl-NAD), a reactive derivative of its coenzyme, NAD.

affinity-purified *or* **affinity-isolated** describing a specified sub-

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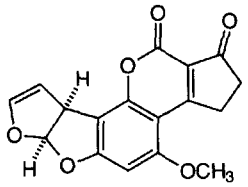
stance, usually a biological macromolecule such as an antigen or antibody, that has been purified (or isolated) by a technique such as **affinity chromatography** or **affinity electrophoresis**, thus implying high purity.

affinity support *an alternative term for* **affinity matrix**.

affinoelectrophoresis *an alternative term for* **affinity electrophoresis**.

aflatoxin any of a group of related and highly toxic secondary metabolites (**mycotoxins**) produced by strains of the moulds *Aspergillus flavus* or *A. parasiticus*, together with further metabolites of these mycotoxins. Their main structural feature is a fused coumarin–bis(dihydrofuran) ring system. The most important are aflatoxins B_1, B_2, G_1, and G_2 — so designated from the colour of their fluorescence (B, blue; G, green). The mycotoxins are produced naturally by the moulds growing on various seed crops, especially groundnuts (peanuts), and certain cereals (e.g. maize) during storage under moist conditions. They are acutely toxic and highly carcinogenic to many species of animals (probably including humans), and are responsible for turkey X disease. The main organ affected is the liver; aflatoxin B_1 is the most potent hepatocarcinogen known. The term is derived as a contraction of *A. flavus* toxin.



aflatoxin B_1

AFLP *abbr. for* amplification fragment length polymorphism. The use of the **polymerase chain reaction** to amplify DNA in the study of **restriction fragment length polymorphism**.

A form **1** A form of DNA (*abbr.*: A-DNA *or* DNA-A); the molecular conformation adopted by fibres of the sodium salt of duplex DNA at a relative humidity of 75% or less. It consists of a right-handed double helix containing about 11 nucleotide residues per turn, with the planes of the base pairs inclined at about 70° to the axis of the helix. Unlike the **B form** of DNA it has a large hole (≈0.8 nm diameter) at the axis and a very deep major groove. *See also* **C form**, **Z form**. **2** A form of RNA (*abbr.*: A-RNA); the molecular conformation of double-stranded regions of RNA that is favoured at low-salt concentrations and moderate temperatures; it resembles the A form of DNA. (*see* def. 1).

AFP *abbr. for* α-fetoprotein.

Ag **1** *abbr. for* antigen. **2** *symbol for* silver.

AGA **1** a codon in non-mitochondrial mRNA for L-arginine. **2** a codon in human mitochondrial mRNA for chain termination. **3** *abbr. for N*-acetylglutamic acid.

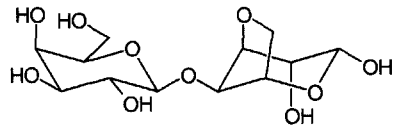
agamic reproduction *see* **asexual reproduction**.

agamogeny the development of a new individual from a single cell. *Compare* **vegetative reproduction**.

agar *or* **agar-agar** a complex sulfated galactan extracted from certain seaweeds, especially *Gelidium* and related genera. The two main components are **agarose** and **agaropectin**. Agar forms an aqueous gel suitable for the solidification of microbiological culture media and for use as a support medium in zone electrophoresis or (immuno)diffusion techniques. It is not metabolized by most organisms. The gelling temperature varies from about 25 to 35 °C for different types of preparation. The gel is then stable to about 90 °C.

agar-diffusion method a method for determining the sensitivity of a microorganism to an antimicrobial drug. The zone of growth inhibition is measured around a ditch, hole, or a filter-paper disk containing the drug and located on an agar culture medium seeded with the microorganism in question.

agarobiose 4-*O*-*β*-D-galactopyranosyl-3,6-anhydro-L-galactose; a **disaccharide** that forms the basic unit of **agarose**.



agarobiose

agaropectin a charged component of **agar** consisting of a mixture of polysaccharides containing D-galactose, 3,6-anhydro-L-galactose, and monoesterified sulfuric acid units. Samples from some algae may contain other components such as pyruvate, L-arabinose, and D-glucuronate units.

agarose an essentially uncharged component of **agar** comprising a ≈120 kDa alternating carbohydrate polymer. It consists of -3)D-Gal*p*-(*β*1-4)-3,6An-L-Gal*p*(*α*1- repeating units, containing small amounts of ionized sulfate and pyruvate groups. It is widely used as a matrix in zone and immunoelectrophoresis, immunodiffusion, and gel filtration and affinity chromatography. *See also* **agarobiose**.

AGC a codon in mRNA for L-serine.

agenized flour *see* **methionine sulfoximine**.

AGG **1** a codon in non-mitochondrial mRNA for L-arginine. **2** a codon in human mitochondrial mRNA for chain termination.

agglutinate **1** to adhere or cause to adhere. **2** to cause the clumping of cells, particles, etc., or to undergo such clumping.

agglutination **1** the act or process of adhering. **2** the process in which suspended cells or other **antigen** coated particles clump together when **antibody** is added due to an antigen–antibody reaction. **3** the result of such a process. *See also* **agglutinin**.

agglutinin an **antibody** that has the ability to agglutinate the corresponding antigen, e.g. when the antigen is present on the surface of a suspended cell or other particle.

agglutinogen an **antigen**, usually particulate, that stimulates the production of **agglutinin**.

aggrecan the major proteoglycan of cartilage. It has approximately one **glycosaminoglycan** chain for every 20 amino-acid residues, and a total mass of about 3 MDa. It assembles with glycosaminoglycans, especially hyaluronan, into aggregates several micrometres in diameter. Example (of protein precursor) from human juvenile cartilage chondrocyte: database code HUMAGPRO, 2316 amino acids (238.97 kDa). *See also* **versican**.

aggregate **1** formed of separate units or particles collected into a whole or into larger units. **2** an assemblage or sum of many separate units or particles. **3** to form or be formed into a single body or larger body.

aggregation **1** the process of forming an **aggregate** (def. 2). **2** a cluster or group of particles held together into larger units.

aggregation number the number of monomers of an amphipathic substance that form a micelle under any particular conditions.

aggressin a diffusible nontoxic substance produced by a microorganism that promotes the invasive power of the microorganism in the host.

aglucon *or (formerly)* **aglucone** an **aglycon** derived from a glucoside (i.e. where the sugar moiety was a glucose residue).

aglycon *or* **aglucon** *or (formerly)* **aglycone** *or* **aglucone** the part

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of any **glycoside** that remains after the sugar moiety has been chemically or enzymically removed.

agmatine 1-amino-4-guanidobutane; a putative endogenous ligand for **imidazoline receptors** synthesized from arginine by the enzyme arginine decarboxylase (EC 4.1.1.19). In some invertebrates e.g. the sponge *Geodia gigas* and some cephalopods, the guanidine group can undergo phosphorylation to phosphoagmatine, which acts as a **phosphagen**.

agnotobiotic pertaining to the growth of organisms of a single species in the presence of one or more other species of which at least one is unknown. *Compare* **synxenic**.

+agogue *or (US)* **+agog** *suffix* denoting an agent that elicits or enhances the secretion of the indicated substance. [from the Greek *agōgos*, leading, drawing forth.] —**+agogic** *adj.*

agonist any ligand, especially a drug or hormone, that binds to receptors and thereby alters the proportion of them that are in an active form, resulting in a biological response. A conventional agonist increases this proportion, whereas an **inverse agonist** reduces it. *See also* **full agonist**, **partial agonist**. *Compare* **antagonist**. —**agonistic** *adj.*

Agranoff's turtle a zoomorphic mnemonic for avoiding the confusion that has tended to occur over the numbering of the carbon atoms of *myo*-inositol and its chiral derivatives, especially when their Haworth projections are converted into diagrams representing their normal chair conformations. The chair conformation of the parent compound is likened to a turtle, with its body corresponding to the C_6 ring, its coplanar limbs and tail representing the five equatorial hydroxyl groups, and its erect head the axial hydroxyl group. The turtle is viewed from above; then, for derivatives named as members of the D series, numbering of the turtle's appendages proceeds counterclockwise, commencing with its right front paw (i.e. its *dextro* 'hand'), which is designated 1D; its head becomes 2D, its left front paw is 3D, and so on around its body. Conversely, numbering of the L series of derivatives commences with the left front paw (the *laevo* 'hand'), designated 1L, and then proceeds clockwise, the head becoming 2L, and so on. [After its originator Bernard William Agranoff (1926–), who devised it in 1978.]

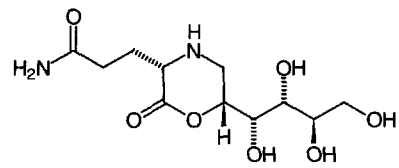
agrin a component of the synaptic basal lamina that causes aggregation of acetylcholine receptors and acetylcholinesterase on the surface of muscle fibres of the neuromuscular junction. It occurs in embryonic nervous tissue and muscle, especially during early development. At least five different forms arise by alternative splicing; they differ in their acetylcholine receptor clustering activity. An **EGF**-like domain is present. Example (precursor) from rat: database code AGRI_RAT, 1959 amino acids (208.41 kDa).

Agrobacterium a genus of Gram-negative aerobic rod-shaped soil bacteria. Most strains can initiate formation of galls in plants (*see* **crown-gall disease**). A feature of the infection of plants by *Agrobacterium* species is that the bacterium can subvert the host plant tissue to produce amino acids known as **opines**, which the bacterium can use as an energy, carbon, and nitrogen source. The type of opine produced is determined by the bacterial strain. Continued presence of the bacteria is not necessary for transformation of the cells of the host plant. Transformation by *Agrobacterium tumefaciens* has been shown to be due to large plasmids (140 – 235 kb). These are known as tumour-inducing or Ti plasmids, and they have been exploited in the production of **transgenic** plants.

agrochemical a chemical that is used in agriculture or horticulture, especially as a biocide, fertilizer, etc.

agroclavine 8,9-didehydro-6,8-dimethylergoline; a nonpeptide **ergot** alkaloid.

agropine an **opine**; a rare amino-acid derivative that is produced by a certain type of crown-gall tumour. The genes responsible for its synthesis are part of the T-DNA from a **Ti plasmid**. *See also* **crown-gall disease**.



agropine

AGU a codon in mRNA for L-serine.

Ah *abbr. for* aromatic hydrocarbon; the name of a genetic locus in higher organisms that governs biological responses to some aromatic hydrocarbons. The proteins it encodes include cytochrome P450 1A1, a liver microsomal monooxygenase that oxidizes a variety of unrelated compounds, including xenobiotics such as the environmental carcinogens, benzo[a]pyrene and 3-methylcholanthrene. This enzyme is induced by these compounds and, more potently, by polychlorinated biphenyls such as 2,3,7,8-tetrachlorodibenzo-*p*-dioxin (TCDD), acting through the **Ah receptor**. The 5′-flanking region of the gene for this enzyme contains several short sequence motifs known as **xenobiotic response elements** (XREs).

ahnak a human gene that encodes a giant protein of ≈700 kDa with a large internal domain (≈4300 amino acids) of highly conserved repeated sequences, much of which are 128 amino-acid residues in length and contain a heptad repeat. The ahnak protein is found in human nuclei and is of unknown function. [From Hebrew *Ahnak,* giant.]

Ah receptor *abbr. for* aryl hydrocarbon receptor; a protein encoded by the ***Ah*** gene that binds a number of aryl hydrocarbons and mediates their biochemical and toxic effects. It is activated when it binds a ligand, and then translocates from the cytoplasm to the nucleus, where it is believed to enhance gene transcription by binding to the **xenobiotic-response element** sequence. It contains a basic helix-turn-helix motif; the DNA-binding form is a heterodimer of this protein and **ARNT**. Example (precursor) from human: database code AHR_HUMAN, 808 amino acids (91.62 kDa).

εAhx *or (formerly)* **εAcp** *symbol for* a residue of the ε-amino acid 6-aminohexanoic acid (formerly known as ε-aminocaproic acid).

aHyl *symbol for* a residue of the α-amino acid L-allohydroxylysine; *threo*-5-hydroxy-L_s-lysine.

AIB *abbr. for* 2-aminoisobutyric acid.

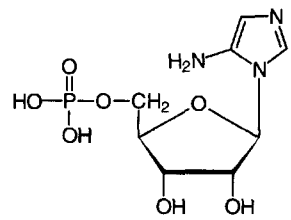
AICAR *abbr. for* 5-amino-4-imidazolecarboxamide ribonucleotide (an intermediate in **purine biosynthesis**).

AICAR transformylase *see* **phosphoribosylaminoimidazolecarboxamide formyltransferase**.

AIDS *abbr. for* acquired immunodeficiency syndrome.

alle (Alle) *symbol for* a residue of the α-amino acid L-alloisoleucine, (2*S*,3*R*)-2-amino-3-methylpentanoic acid.

AIR *abbr. for.* for 5-aminoimidazole ribonucleotide, an intermediate in **purine biosynthesis**.



AIR carboxylase *see* **phosphoribosylaminoimidazole carboxylase**.

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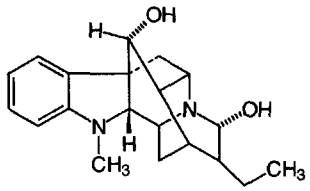
air-lift bioreactor a bioreactor in which the reaction medium is kept mixed and gassed by the introduction of air or another gas at the base of a column-like reactor.

ajmaline ajmalan-17,20-diol; an alkaloid from the roots of *Rauwolfia serpentina*. It is used clinically as an antihypertensive and antiarrhythmic, having the effect of normalizing heart rhythm.



AK *(in clinical biochemistry) abbr. for* adenylate kinase.

AKAP *abbr. for* A-kinase anchor protein *or* cAMP-dependent protein kinase anchor protein; a protein that anchors the kinase to cytoskeletal and/or organelle-associated proteins, targeting the signal carried by cyclic AMP to specific intracellular effectors. The N-terminal region, which is highly basic, is required for interaction with **calmodulin**. Example (human): database code AK79_HUMAN, 427 amino acids (47.02 kDa).

akaryotic describing a cell without a nucleus.

akee *a variant spelling of* **ackee**.

AKH *abbr. for* adipokinetic hormone.

A-kinase an enzyme that phosphorylates target proteins in response to a rise in intracellular **cyclic AMP**. *See* **cyclic AMP-dependent protein kinase**.

Akt the mouse or human homologue of v-*akt*, the oncogene of the transforming retrovirus AKT8. v-*akt* encodes a serine/threonine protein kinase that contains an SH2 domain. Database code KAKT_MLVAT, 501 amino acids (57.87 kDa).

al+ *prefix* denoting an acyclic monosaccharide or monosaccharide derivative. *See also* ***aldehydo-***.

+al *suffix* denoting an unbranched acyclic mono- or dialdehyde.

Al *symbol for* aluminium.

Ala *symbol for* a residue of the α-amino acid L-alanine, 2-aminopropanoic acid (alternative to A).

βAla *symbol for* a residue of the β-amino acid β-alanine, 3-aminopropanoic acid.

ALA *or* **dALA** *abbr. for* δ-aminolevulinate.

Ala AT *or* **ALAT** *(in clinical biochemistry) (formerly) abbr. for* alanine aminotransferase. ALT is preferred.

ALA dehydratase *see* **porphobilinogen synthase**.

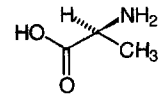
alamethicin a linear ionophorous antibiotic polypeptide containing a high proportion of 2-methylalanine residues and blocked at both ends. *See also* **peptaibophols**.

Ac-2-MeAla-L-Pro-2-MeAla-L-Ala-2-MeAla-L-Ala-
L-Gln-2-MeAla-L-Val-2-MeAla-Gly-L-Leu-
2-MeAla-L-Pro-LVal-2-MeAla-2-MeAla-L-Glu-
L-Gln-L-phenylalaninol

alaninal the aldehyde obtained by reduction of the carboxyl group of alanine.

alaninate **1** alanine anion, the anion $CH_3–CH(NH_2)–COO^-$. **2** any salt containing alanine anion. **3** any ester of alanine.

alanine *the trivial name for* α-aminopropionic acid; 2-aminopropanoic acid; $CH_3–CH(NH_2)–COOH$; a chiral α-amino acid. L-alanine *(symbol*: A *or* Ala), (*S*)-2-aminopropanoic acid, is a coded amino acid found in peptide linkage in proteins; codon: GCA, GCC, GCG, or GCU. In mammals it is a nonessential dietary amino acid and is glucogenic. Residues of D-alanine *(symbol*: D-Ala *or* DAla), (*R*)-2-aminopropanoic acid, are found in cell-wall peptidoglycans of various bacterial species and in other materials, e.g. **cyclosporin**.



L-alanine

***β*-alanine** *symbol*: βAla; *the trivial name for* β-aminopropionic acid; 3-aminopropanoic acid; $H_2N–CH_2–CH_2–COOH$; an achiral β-amino acid. It occurs free in brain and in combination in pantothenate (and hence in coenzyme A) and in the isopeptides anserine and carnosine, but it is not a constituent of proteins. It has an inhibitory effect on the central nervous system.

alanine cycle *see* **glucose–alanine cycle**.

***β*-alanine–oxoglutarate aminotransferase** *see* **4-aminobutyrate transaminase**.

alanine transaminase *abbr. (in clinical biochemistry)*: ALT; EC 2.6.1.2; *systematic name*: L-alanine:2-oxoglutarate aminotransferase; *other names*: glutamic–pyruvic transaminase; glutamic–alanine transaminase. An enzyme that catalyses the reversible reaction:

L-alanine + 2-oxoglutarate = pyruvate + L-glutamate.

Widely distributed in all tissues and organisms, it is a pyridoxal-phosphate enzyme. Example, cytoplasmic isoform: database code ALAT_HUMAN, 495 amino acids (54.38 kDa). In clinical chemistry its assay alongside aspartate transaminase (AST) normally present in plasma in higher concentrations, may be useful as an indicator of liver damage, as levels of ALT are higher in liver than those of AST, in contrast to other tissues. In hepatitis, plasma levels of ALT may exceed those of AST.

alaninium alanine cation, $CH_3–CH(NH_3^+)–COOH$.

alanino the alkylamino group, $CH_3–CH(COOH)–NH–$, derived from alanine.

alaninol the alcohol obtained by the successive reduction of the carboxyl group of alanine.

alanyl the acyl group, $CH_3–CH(NH_2)–CO–$, derived from alanine.

alarmone any signal molecule that serves to reorient a cell's economy in response to stress. Such molecules include ppGpp, which is produced, e.g., in microorganisms, in response to growth-rate limitation caused by amino-acid stress and acts to correct this in various ways, and diadenosine tetraphosphate (ApppA), which stimulates proliferation when DNA replication is halted at a replication fork.

ALA synthetase *see* **5-aminolevulinate synthase**.

ALAT *See* **Ala AT**.

albinism an inherited metabolic disorder in which there appears to be a complete or nearly complete failure to form melanin. It was first listed in 1908 by the British physician Archibald Garrod (1857–1936) in his lecture entitled 'Inborn Errors of Metabolism'. In some cases it is due to a deficiency of 'tyrosinase' (**monophenol monooxygenase**), but other types are known in which this enzyme is present, and for which the precise cause is unknown.

albumin any of a group of globular proteins that are soluble in distilled water and solutions of half-saturated ammonium sulfate, but insoluble in fully saturated ammonium sulfate solutions. **Serum albumin**, the major protein of serum, has a good binding capacity for water, Ca^{2+}, Na^+, K^+, fatty acids, hormones, bilirubin, and drugs. Its main function is the regulation of the colloidal osmotic pressure of blood; it has structural similarity to **α-fetoprotein** and **vitamin D binding protein**. Example (precursor) from human: database code ALBU_HUMAN, 609 amino acids (69.29 kDa). *See also* **endosperm albumin**, **lactalbumin**, **ovalbumin**, **serum albumin**. [The name origi-

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nates from Latin *albus,* white, as it exists in nearly pure form in egg-white, from which it was easily obtained by the ancients.]

albuminoid 1 of or relating to an **albumin**. 2 *an alternative name for* **scleroprotein**.

albuminuria the presence of excessive amounts of protein in the urine. It is usually a sign of renal disease.

albuterol *see* **salbutamol**.

Alcalase *the proprietary name for* a proteolytic enzyme preparation obtained by fermentation of a strain of *Bacillus subtilis*. It is characterized by stability and activity at high temperatures and alkaline pH values, and is used in enzymic laundering and various industrial processes.

alcapton 2,5-dihydroxyphenylacetic acid. *See* **alcaptonuria**, **homogentisate**.

alcaptonuria *or* **alkaptonuria** a rare hereditary metabolic disease, usually due to an autosomal recessive gene, in which the enzyme homogentisic acid oxidase (homogentisate 1,2-dioxygenase, EC 1.13.11.5) is virtually absent. This leads to the inability to metabolize further the homogentisate produced by the normal metabolism of phenylalanine and tyrosine. Homogentisate therefore accumulates in the body and is excreted in the urine, which gradually turns dark as homogentisate is oxidized to a melanin-like product – a process speeded up at an alkaline pH.

alcohol 1 any of a class of alkyl compounds containing a hydroxyl group. An alcohol is called primary, secondary, or tertiary according to whether the carbon atom bearing the hydroxyl group is itself attached to one, two, or three other carbon atoms. 2 specifically, ethyl alcohol, ethanol. *See also* **absolute alcohol**. —**alcoholic** *adj., n.*

alcohol dehydrogenase any of the nicotinamide-nucleotide-linked dehydrogenase enzymes of groups EC 1.1.1.1 (NAD^+) or EC 1.1.1.2 ($NADP^+$) that catalyse the oxidation of alcohols to aldehydes. These are zinc proteins. Also EC 1.1.1.71, alcohol dehydrogenase [$NAD(P)^+$]; *other name*: retinal reductase; EC 1.1.99.8, alcohol dehydrogenase (acceptor), a quinoprotein. Examples: alcohol dehydrogenase I from *Saccharomyces cerevisiae*: database code ADH1_YEAST, 347 amino acids (36.66 kDa); alcohol dehydrogenase 6 (human): database code ADH6_HUMAN, 368 amino acids (39.03 kDa).

alcoholic fermentation the conversion of glucose to ethanol by a group of reactions that are characteristic of yeast.

alcohol oxidase *abbr.*: AOX *or* **methanol oxidase** *abbr.*: MOX; EC 1.1.3.13; a flavoprotein (FAD) enzyme that catalyses the oxidation by dioxygen of a primary alcohol to the corresponding aldehyde. It is important in methylotrophic yeasts, in which it is the first enzyme in the pathway for utilization of methanol, converting this to formaldehyde, thence to CO_2.

alcoholysis the solvolysis of a covalent derivative of an acid by a reaction in which one of the products combines with the H atom of an alcohol's hydroxy group and the other product with the alcohol's alkoxy group.

aldaric acid any dicarboxylic acid formed by oxidation of both terminal groups of an **aldose** to carboxyl groups. There are three tetraric acids (D-, L-, and *meso*-tartaric acids), four pentaric acids (D- and L-arabinaric acids, xylaric acid [*meso*], and ribaric acid [*meso*]), and ten hexaric acids (D- and L-glucaric acids, D- and L-idaric acids, D- and L-mannaric acids, D- and L-talaric acids, allaric acid [*meso*], and galactaric acid [*meso*]).

aldehyde 1 *an alternative name for* the **formyl** group, –CHO. 2 any organic compound with the formula R–CH=O. *Compare* **ketone**. —**aldehydic** *adj.*

aldehyde dehydrogenase any enzyme that catalyses the oxidation of an aldehyde group to a carboxylic acid. Many examples are known, acting specifically on a wide range of substrates. Those acting on aliphatic aldehydes are divided into four classes. Class 1, or Ald C, are tetrameric cytosolic enzymes, and include aldehyde dehydrogenase (NAD^+), EC 1.2.1.3; *systematic name*: aldehyde:NAD^+ oxidoreductase; an enzyme of wide specificity. Example from human: database code DHAC_HUMAN, 500 amino acids (54.73 kDa). This EC designation also includes Class 2 enzymes, or Ald M, which are tetrameric mitochondrial enzymes. Class 3, or Ald D, are dimeric cytosolic enzymes, and include aldehyde dehydrogenase [$NAD(P)^+$], EC 1.2.1.5; *systematic name*: aldehyde:$NAD(P)^+$ oxidoreductase. Example from human: database code DHAP_HUMAN, 453 amino acids (50.35 kDa).

aldehyde ferredoxin oxidoreductase an enzyme that catalyses the reversible oxidation of aldehydes to the corresponding carboxylic acid, using ferredoxin as an electron acceptor. Containing tungsten, molybdopterin molecules, and Fe_4S_4 clusters, the enzyme has remarkable thermostability. Its 3-D structure is known.

aldehydo- *abbr.*: al-; *prefix* designating an uncyclized monosacccharide or monosaccharide derivative. It is used in (semi)systematic nomenclature to stress the acyclic nature of such compounds. *Compare* ***keto-***.

aldimine any **imine** that is an analogue of an aldehyde; the general structure is RCH=NR where R may be any organyl group or H. *Compare* **ketimine**.

alditol any polyhydric alcohol derived from the acyclic form of a **monosaccharide** by reduction of its aldehyde or keto group to an alcoholic group. Older names for these compounds include glycitol and sugar alcohol.

aldo+ *prefix* indicating aldehydic; e.g. aldohexose.

aldoketose any monosaccharide derivative containing both a (potential) aldehydic carbonyl group and a (potential) ketonic carbonyl group.

aldol 1 any organic compound that is both an aldehyde and an alcohol, especially where the two functions are separated by two linked carbon atoms in accordance with the general structure: HO–C–C–CH=O. 2 *the trivial name for* acetaldol (3-hydroxybutanal) a compound formed by the self-condensation of two acetaldehyde molecules.

aldolase 1 *a generic name for* nearly every enzyme of the subsubclass EC 4.1.2, the aldehyde-lyases, enzymes catalysing aldol condensations and their reversal. 2 *abbr. (in clinical biochemistry)*: ALS; *common name for* the enzyme **fructose-bisphosphate aldolase**; EC 4.1.2.13; *systematic name*: D-fructose-1,6-bisphosphate D-glyceraldehyde-3-phosphate-lyase; *other name*: fructose-1,6-bisphosphate triosephosphate-lyase. An enzyme that catalyses the reversible fission of D-fructose 1,6-bisphosphate to glycerone phosphate and D-glyceraldehyde 3-phosphate. It acts also on (3*S*,4*R*)-ketose 1-phosphates. In mammals three isoenzymes are known: aldolase A in muscle; aldolase B in liver, kidney, and small intestine; and aldolase C in brain. All three isoenzymes catalyse the reversible splitting of both D-fructose 1,6-bisphosphate and D-fructose 1-phosphate, but with different relative limiting rates; liver aldolase B shows approximately the same limiting rate with both substrates, while aldolase A and aldolase C show, respectively, a 50-fold and a 10-fold lower maximal activity with fructose 1-phosphate than with fructose 1,6-bisphosphate. Each is of ≈160 kDa and is composed of four subunits, which are immunologically distinct in the three isoenzymes. Examples, aldolase A from *Mus musculus*: database code ALFA_MOUSE, 363 amino acids (39.22 kDa); aldolase from *Pisum sativum*: database code ALF1_PEA, 357 amino acids (38.44 kDa). Three different but related aldolase genes (probably formed from a single ancestral gene) have been identified; in humans the aldolase-A gene is in chromosome 16, the aldolase-B gene is present as a single copy in chromosome 9, and the aldolase-C gene is in chromosome 17. *See also* **hereditary fructose intolerance**.

aldol condensation the base-catalysed addition reaction of two aldehydes or an aldehyde and a ketone to form an **aldol** (def. 1).

aldonic acid a monocarboxylic acid having a chain of three or more carbon atoms and formally derived from an **aldose** by oxidation of the aldehydic group.

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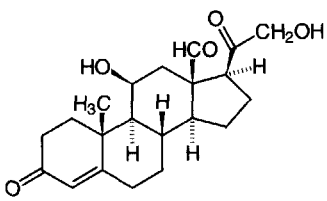
aldopentose any of the eight possible five-carbon-atom **aldoses**.

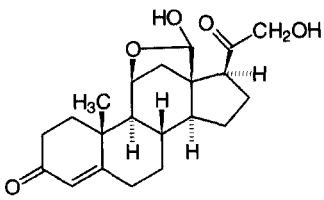
aldopyranose any **aldose** in the **pyranose** form.

aldose a monosaccharide in which the (potential) carbonyl group is terminal (i.e. aldehydic). The term is frequently modified to indicate the number of carbon atoms in the chain, as in aldotriose, aldotetrose, etc.

aldosterone 11β,21-dihydroxy-3,20-dioxopregn-4-en-18-al; the most powerful naturally occurring mineralocorticoid hormone, originally named **electrocortin** by its discoverers Sylvia Simpson and James Tait in 1954. The name was changed to aldosterone after its structure had been determined by **Reichstein** in 1953. It exists in solution as an equilibrium mixture of the aldehyde and the hemiacetal formed with the hydroxyl at position 11. Produced by the cells of the zona glomerulosa of the adrenal cortex, its main action is to increase reabsorption of sodium ions by the distal renal tubules and thus to regulate water and electrolyte metabolism. The biosynthesis of aldosterone is stimulated by angiotensin II (*see* **angiotensin**, **renin–angiotensin system**), **corticotropin**, and increased potassium-ion concentrations. 11-Deoxycorticosterone is converted into aldosterone by **aldosterone synthase**. Aldosterone exerts its effects through binding to cytosolic receptors. The resulting complex is transferred to the nucleus, where it acts to stimulate production of mRNA for sodium transport proteins. The action is thus on a timescale of many minutes.



aldehyde form



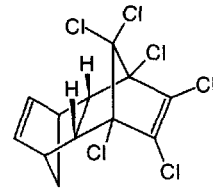
hemiacetal form

aldosterone synthase EC 1.14.15.4; *recommended name*: steroid 11β-monooxygenase; *other names*: cytochrome P450 11B2; steroid 18-hydroxylase; P450C18. A heme–thiolate enzyme that converts 11-deoxycorticosterone to aldosterone, by successive hydroxylations at the 11β and 18 positions. Reduced adrenodoxin is a reactant, being converted to oxidized adrenodoxin. Example, human (precursor): database code CPN2_HUMAN, 503 amino acids (57.58 kDa).

aldotetrose any of the four possible four-carbon-atom **aldoses**.

aldotriose either D- or L-glyceraldehyde; *see* **aldose**.

aldrin 1,2,3,4,10,10-hexachloro-1,4,4a,5,8,8a-hexahydro-1,4:5,8-dimethanonaphthalene; an organochlorine compound formerly used as an insecticide, but now banned in certain countries on account of its toxicity.



aldrin

aleuron *or* **aleurone** **1** granules of insoluble protein found in plant cells, especially in the seeds of cereals, where they appear to act as storage material. **2** the single layer of cells on the outside of the endosperm of cereal seeds containing such granules. Translocated **gibberellins** stimulate the cells to synthesize α-amylase, which is secreted into the endosperm to hydrolyse the stored starch.

aleuroplast any colourless **plastid** or **leukoplast** storing protein. Aleuroplasts are found in plant cells, particularly seeds.

alexin *or* **alexine** *former term for* **complement**; hence **alexinated** means treated with complement.

ALG *abbr. for* anti-lymphocyte globulin.

alga (*pl.* **algae**) any of a group of simple eukaryotic photosynthetic protists. They may be unicellular or multicellular, and are generally aquatic. The prokaryotes formerly called blue-green algae are now known as **cyanobacteria**.—**algal** *adj.*

algicide any chemical agent that selectively kills algae.

algin the sodium salt of **alginic acid**

alginate lyase EC 4.2.2.3; *recommended name*: poly(β-D-mannuronate) lyase; *systematic name*: poly(β-D-1,4-mannuronide) lyase. An enzyme that catalyses a reaction resulting in eliminative cleavage of polysaccharides containing β-D-mannuronate residues to give oligosaccharides with 4-deoxy-α-L-*erythro*-hex-4-enopyranuronosyl groups at their ends. Example from *Pseudomonas aeruginosa*: database code PSEALGL, 367 amino acids (40.78 kDa).

alginic acid a hydrophilic polysaccharide (≈240 kDa) occurring in brown algae (brown seaweeds), especially the Californian giant kelp (*Macrocystis pyrifera*) and horsetail kelp (*Laminaria digitata*). Sodium alginate is used commercially as an emulsifier and thickener in foodstuffs, pharmaceuticals, etc. It has an interrupted structure of stretches of α1-4-linked α-L-gulopyranosyluronic acid residues, stretches of β1-4-linked β-D-mannopyranosyluronic acid residues, and stretches where both uronic acids occur in alternating sequence. Similar glycans are secreted by some bacteria.

algorithm any systematic mathematical procedure that allows a problem to be solved in a finite number of steps. *Compare* **heuristic**, **stochastic**.

alicyclic describing an organic compound derived from a saturated cyclic hydrocarbon. *Compare* **aliphatic**, **aromatic**.

aliphatic describing organic compounds in which the carbon atoms form open (noncyclic) chains. *Compare* **alicyclic**, **aromatic**.

aliquant one of a number of unequal parts of a whole.

aliquot one of number of equal parts of a whole; often used loosely, and erroneously, for a sample.

alizarin 1,2-dihydroxyanthraquinone; the **aglycon** of **ruberythric acid**.

alkalemia *or (esp. Brit)* **alkalaemia** a condition in which there is increased alkalinity (i.e. lowered hydrogen-ion concentration and hence raised pH) of the blood. *Compare* **acidemia**, **alkalosis**.

alkali any of a class of bases that neutralize acids and are themselves neutralized by acids, and form caustic and/or corrosive aqueous solutions. The term is applied in particular to hy-

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droxides of the **alkali metals**, though the term is often extended to other substances with similar though weaker properties.

alkali metal any element of group 1 of the IUPAC **periodic table**; the group comprises lithium (Li), sodium (Na), potassium (K), rubidium (Rb), cesium (Cs), and francium (Fr).

alkaline **1** having the properties of an **alkali**; basic. **2** describing an aqueous solution having a pH > 7.

alkaline earth any metallic element belonging to group 2 of the IUPAC **periodic table**; the group comprises beryllium (Be), magnesium (Mg), calcium (Ca), strontium (Sr), barium (Ba), and radium (Ra).

alkaline phosphatase EC 3.1.3.1; *systematic name*: orthophosphoric monoester phosphohydrolase (alkaline optimum); *other names*: alkaline phosphomonoesterase; phosphomonoesterase; glycerophosphatase. An enzyme that catalyses the hydrolysis of orthophosphoric monoester to an alcohol and orthophosphate. The cofactors are zinc and magnesium. In human plasma the level is raised in the last trimester of pregnancy. Plasma levels may also be greatly elevated in cases of Paget's disease of bone, osteomalacia, and cirrhosis or biliary obstruction; levels may become moderately elevated in other types of bone disease. The assay of tissue-specific isoenzymes increases the value of these estimations; e.g. the placental isoenzyme is elevated in plasma in testicular seminoma. The normal range in human plasma is 30–90 IU L^{-1}. Example from intestine (bovine): database code PPBI_BOVIN, 44 amino acids (4.77 kDa); example from *Escherichia coli* (precursor): database code PPB_ECOLI, 471 amino acids (49.38 kDa).

alkaline tide the slight increase in plasma and urine pH that occurs after meals. It is believed to be due to withdrawal of hydrogen ions from the blood during the formation of gastric HCl.

alkali reserve *or* **alkaline reserve** *a term formerly used to denote* the bicarbonate-CO_2 extractable from blood plasma.

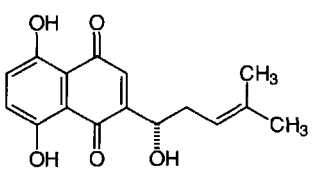
alkaloid any member of a broad group of nitrogen-containing basic organic compounds present in various dicotyledonous plants and some fungi. Although only about 5% of the world's plant species have so far been examined, they have yielded over 2000 different alkaloids. Heterocyclic alkaloids derived from amino acids are termed **true alkaloids**. Alkaloids with and without heterocyclic rings and not derived from amino acids are termed **pseudoalkaloids**; in these the carbon skeleton is usually isoprenoid derived. Alkaloids often have marked and specific pharmacological activity.

alkalosis a clinical condition in which total base excess or total acid deficit has the potential to cause decreased hydrogen-ion concentration (i.e. raised pH) in the blood, in the absence of compensating biochemical and physiological changes.

alkane any saturated aliphatic hydrocarbon compound.

alkanet the plant, *Alkanna tinctoria*, and its root, which contains the pigment **alkannin**.

alkannin (*S*)-5,8,-dihydroxy-2-(1-hydroxy-4-methyl-3-pentenyl)-1,4-naphthalenedione; a red pigment derived from the root of the alkanet plant, and used as a dye in cosmetics and food. The (+)(*R*) enantiomer is also a natural product, **shikonin**, and the racemate is known as shikalkin.



alkaptonuria *a variant spelling of* **alcaptonuria**.

alkatriene any unsaturated aliphatic hydrocarbon containing two (conjugated or unconjugated) double bonds.

alkatrienyl any group derived from an alkatriene by removal of a hydrogen atom.

alkenyl any group derived from an alkene by removal of a hydrogen atom.

1-alkenyl-2-acylglycerol cholinephosphotransferase EC 2.7.8.22; an enzyme that catalyses the formation of the plasmalogen, plasmenylcholine (i.e. 1-alkenyl-2-acylglycerophosphocholine), from CDPcholine and 1-alkenyl-2-acylglycerol with release of CMP.

1-alkenylglycerophosphocholine *O*-acyltransferase EC 2.3.1.104; an enzyme that catalyses the formation of the plasmalogen, plasmenycholine (i.e. 1-alkenyl-2-acylglycerophosphocholine) from acyl-CoA and 1-alkenylglycerophosphocholine with release of CoA.

alkenylglycerophosphocholine hydrolase EC 3.3.2.2; *other name*: lysoplasmalogenase; a phospholipase involved in the turnover of **plasmalogens**. It catalyses the hydrolysis of 1-(1-alkenyl)-*sn*-glycero-3-phosphocholine to an aldehyde and *sn*-glycero-3-phosphocholine.

1-alkenylglycerophosphoethanolamine *O*-acyltransferase EC 2.3.1.121; an enzyme that catalyses the formation of the **plasmalogen**, 1-alkenyl-2-acyl-glycerophosphoethanolamine, from acyl-CoA and 1-alkenylglycerophosphoethanolamine with release of CoA.

alkenylglycerophosphoethanolamine hydrolase EC 3.3.2.5; a phospholipase enzyme involved in the turnover of **plasmalogens**. It catalyses the hydrolysis of 1-(1-alkenyl)-*sn*-glycero-3-phosphoethanolamine to an aldehyde and *sn*-glycero-3-phosphoethanolamine.

alkyl any group derived from an alkane by the removal of one hydrogen atom. Alkyl groups are often designated by the symbol R.

alkylating agent any of a group of compounds that react with another compound so as to introduce an alkyl group into the second compound.

alkylation the process of replacing a hydrogen atom in a compound by an alkyl group.

1-alkylglycerophosphocholine *O*-acetyltransferase EC 2.3.1.67; an enzyme that catalyses the formation of 1-alkyl-2-acetyl-*sn*-glycero-3-phosphocholine (*see* **platelet-activating factor**) from acetyl-CoA and 1-alkyl-*sn*-glycero-3-phosphocholine with release of CoA. *See also* **1-alkylglycerophosphocholine *O*-acyltransferase**.

1-alkylglycerophosphocholine *O*-acyltransferase EC 2.3.1.63; an enzyme that catalyses the formation of the **ether lipid**, 1-alkyl-2-acyl-*sn*-glycero-3-phosphocholine, from acyl-CoA and 1-alkyl-*sn*-glycero-3-phosphocholine with release of CoA.

***O*^{6}-alkylguanine alkyltransferase** *see* ***O*^{6}-methylguanine**.

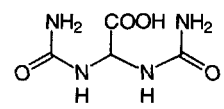
alkyne any unsaturated aliphatic hydrocarbon compound containing one or more triple bonds.

alkynyl any group derived from an **alkyne** by the removal of one hydrogen atom.

All *symbol for* allose.

all+ *see* **allo+**.

allantoic acid *or* **diureidoacetate** the end product of **purine** metabolism in mammals and some fish, formed from **allantoin** by a hydrolytic reaction. Most fish metabolize allantoic acid further to urea and glyoxalate. It is widely distributed in plants as an important source of stored nitrogen.



allantoin (2,5-dioxo-4-imidazolidinyl)urea; 5-ureidohydantoin; an intermediate or end product of purine catabolism, formed from uric acid by urate oxidase. In certain animal groups it is converted to allantoic acid.

allele *or* **allelomorph** any of the forms of the same **gene** that occur at the same **locus** on a homologous chromosome but dif-

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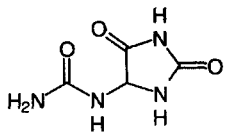
fer in base sequence. Two or more alleles are said to be **allelic** or **allelomorphic** to each other, and if more than two alleles exist in a population, the locus is said to show **multiple allelism**.



allantoin

allele-specific oligonucleotide *abbr.*: ASO; an oligonucleotide that is constructed with a DNA sequence homologous to a specific allele. Two ASOs can be made so that they differ in sequence at only one nucleotide base, thereby distinguishing a mutant allele with a point mutation from its corresponding wild-type allele.

allelic exclusion the process by which a cell uses either the gene from its maternal chromosome or the one from the paternal chromosome, but not both. It seems to occur only in genes that encode antibodies and T-cell receptors. Individual B-lymphocytes display allelic exclusion of their heavy and light IgG genes.

allelomorph *another term for* **allele**.

allelopathic agent any plant excretory product that may be autotoxic or affect neighbouring plants, such as salicylate in *Quercus falcata*.

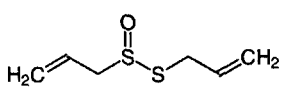
allelozyme any of two or more variants of a particular enzyme (with similar catalytic properties) whose amino-acid sequences are encoded in allelic structural genes (*see* **allele**); a class of **isoenzyme**. *Compare* **multilocus enzyme**.

allergen any **antigen** that stimulates an allergic reaction, inducing a type I hypersensitive reaction. *See* **allergy, hypersensitivity**.

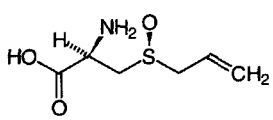
allergic of, relating to, or involving **allergy**.

allergy *or* **allergic reaction** **1** a state of altered (usually increased) reactivity of the body to foreign material. **2** **hypersensitivity**.

allicin 2-propene-1-sulfinothioic acid *S*-2-propenyl ester; an antibacterial compound derived from garlic (*Allium sativum*) and having an odour of garlic.



alliin 3-(2-propenylsulfinyl)-L-alanine; *S*-allyl-L-cysteine sulfoxide; a component of garlic (*Allium sativum*) and other plants that develops an odour of garlic following the action of alliinase (alliin lyase; EC 4.4.1.4).



allitol a *meso*-hexitol; derived formally by reduction of the aldehyde group of either D- or L-allose.

allo+ *or (before a vowel)* **all+** *comb. form* **1** denoting other, dissimilar, different. *Compare* **hetero+** (def. 1), **homo+** (def. 1), **iso+** (def. 1), **xeno+** (def. 1). **2** referring to a dissimilar genome. *Compare* **homo+** (def. 2), **hetero+** (def. 2), **iso+** (def. 2), **xeno+** (def. 2). **3** referring to an isomeric form of an enantiomer of a compound that has more than one pair of enantiomers. *Compare* **iso+** (def. 3), **nor+** (def. 1).

allo+ *prefix* denoting the configuration of a set of four (usually) contiguous >CHOH groups, as in D- or L-allose. *See* **monosaccharide**.

alloantigen an antigen that is part of an animal's self-recognition system, e.g. **major histocompatability complex** molecules. When injected into another animal, they trigger an immune response aimed at eliminating them. *Compare* **alloreactivity**.

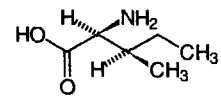
allocystathionine *see* **cystathionine**.

allogeneic *or* **allogenic** describing cells, tissues, organisms, etc. that are of different genetic constitution. *Compare* **heterogenic, homologous**.

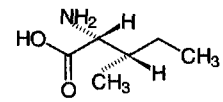
allograft any tissue graft between allogeneic individuals; *i.e.* from a donor of one genotype to a host of another genotype.

allohydroxylysine *see* **hydroxylysine**.

alloisoleucine *trivial name for* α-amino-β-methylvaleric acid; (2*R**,3*S**)-2-amino-3-methylpentanoic acid, CH_3–CH_2–$CH(CH_3)$–$CH(NH_2)$–COOH; an α-amino acid with two chiral centres. Because molecules of alloisoleucine possess a second chiral centre, at C-3, in addition to the chiral centre at C-2 common to molecules of all α-amino acids other than glycine, the enantiomers L-alloisoleucine (*symbol*: aIle), (2*S*,3*R*)-2-amino-3-methylpentanoic acid, and D-alloisoleucine (*symbol*: D-aIle), (2*R*,3*S*)-2-amino-3-methylpentanoic acid, are diastereoisomeric with those of **isoleucine**, (2*R**, 3*R**)-2-amino-3-methylpentanoic acid. L-Alloisoleucine does not occur in peptide linkage in proteins. Residues of D-alloisoleucine are found in the peptidolipid of the actinomycete, *Nocardia esteroides*, and various members of the actinomycin group of antibiotics contain (usually) two residues per molecule.

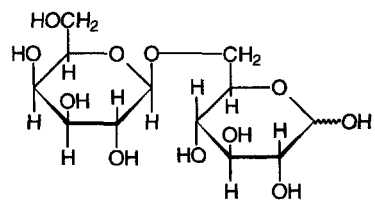


L-alloisoleucine



D-alloisoleucine

allolactose *trivial name for* β-D-galactopyranosyl-(1→6)-D-glucopyranose; an isomer of lactose and the natural intracellular inducer of the ***lac* operon** in *Escherichia coli*.



allomerism a state of similarity in the crystalline structures of substances of different chemical composition. —**allomerous** *adj.*

allometric **1** differing in relative growth rates. **2** of or relating to allometry.

allometry **1** the study of the growth of parts of an organism

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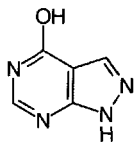
relative to the growth of the whole organism. **2** change in the proportion of any part of an organism occurring during growth.

allomone any chemical substance produced or acquired by an organism that, when it contacts an individual of another species in the natural context, evokes in the receiver a behavioural or developmental reaction adaptively favourable to the transmitter. *Compare* **kairomone**, **pheromone**.

allomorphism variability in the crystalline structure of certain substances having the same chemical composition.

allophycocyanin a **phycobiliprotein** present in small amounts in red algae and cyanobacteria.

allopurinol 4-hydroxypyrazolo[3,4-*d*]pyrimidine; a constitutional isomer of hypoxanthine and a competitive inhibitor of xanthine oxidase (EC 1.2.3.2). It is a synthetic drug used in the treatment of gout and other conditions characterized by raised blood urate content. Patients with gout excrete less urate and more xanthine and hypoxanthine than normal.



alloreactivity the T-cell response to non-self MHC molecules.

all-or-none describing a chemical reaction, or a pharmacological or physiological response, that either occurs to the fullest extent or not at all, depending on the conditions.

allose *symbol*: All; *allo*-hexose; an aldohexose that differs from glucose only in the configuration of the hydroxyl on C-3.

allosteric describing protein molecules that are assumed to possess two or more stereospecifically different, nonoverlapping receptor sites. One of these, the **active site**, binds the substrate; the other, the **allosteric site**, is complementary to the structure of another, or the same, metabolite, the **allosteric effector**, which binds specifically and reversibly. The formation of the enzyme–allosteric effector complex does not activate or deactivate a reaction involving the effector itself; it is assumed only to bring about a discrete reversible alteration of the molecular structure of the protein, called **allosteric transition**. This modifies the properties of the active site, changing one or several of the kinetic parameters that characterize the biological activity of the protein. *See also* **Monod–Wyman–Changeux model**.

allosteric activation any activation of an enzyme by a positive **allosteric effector**.

allosteric constant *symbol*: L; the equilibrium constant for the transition between two forms of an **allosteric** protein in the absence of ligand: $L = T_0/R_0$, where T_0 and R_0 are the concentrations of the less affine T-form and the more affine R-form of the protein, respectively. *See* **Monod–Wyman–Changeux model**.

allosteric effect an effect that arises when the reaction of ligands with one site of any polyvalent molecule affects the reaction of ligand(s) at one or more other sites as a result of conformational changes. The reactions may or may not both be reversible; when they are, and represent equilibria, they are **reciprocal effects** or **linked functions**.

allosteric effector a specific ligand that binds to the allosteric site of a protein with different affinities in the two states of the protein (R and T) in the **Monod–Wyman–Changeux model** of allosteric transition. An effector may be described as positive if it has an activating effect, or as negative if it is inhibitory. *See* **allosteric**. *Compare* **autosteric effector**.

allosteric enzyme designating any enzyme that: (1) contains a site topologically distinct from the active site; (2) shows sigmoid kinetics; (3) occurs at a branch point in a metabolic pathway; and (4) obeys the concerted model for allosteric proteins. Since all these properties may sometimes, but not always, go together, the term is somewhat imprecise.

allosteric inhibition any inhibition of an enzyme by a negative **allosteric effector**.

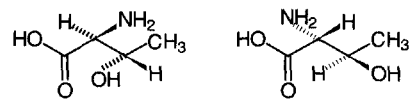
allosteric protein a protein that exhibits **allosterism**. *See also* **allosteric**.

allosteric site *see* **allosteric**.

allosteric transition *see* **allosteric**, **Monod–Wyman–Changeux model**.

allosterism *or* **allostery** a property of an enzyme or other macromolecule by which its principal biological reactivity is modified by the binding of an effector to a site other than the binding site of the principal reactant, thereby bringing about a conformational change in the macromolecule such as to alter its principal reactivity. *See* **allosteric**.

allothreonine *trivial name for* α-amino-β-hydroxybutyric acid; (2*R**,3*R**)-2-amino-3-hydroxybutanoic acid; CH_3–CH(OH)–CH(NH_2)–COOH; an α-amino acid with two chiral centres. Because molecules of allothreonine possess a second chiral centre, at C-3, in addition to the chiral centre at C-2 common to all α-amino acids other than glycine, the enantiomers L-allothreonine (*symbol*: aThr), (2*S*,3*S*)-2-amino-3-hydroxybutanoic acid, and D-allothreonine (*symbol*: D-aThr), (2*R*,3*R*)-2-amino-3-hydroxybutanoic acid, are diastereoisomeric with those of **threonine**, (2*R**,3*R**)-2-amino-3-hydroxybutanoic acid. [*Note*: The enantiomers of allothreonine may also be named semisystematically as derivatives of erythrose: L_s-allothreonine in amino-acid nomenclature is synonymous with 2-amino-2,4-dideoxy-L_g-erythronic acid in carbohydrate nomenclature, and D_s-allothreonine with 2-amino-2,4-dideoxy-D_g-erythronic acid (the subscript letters d or g being added to the configurational prefixes where there might be uncertainty regarding the reference centre of chirality; *see* **D/L convention**).] L-Allothreonine does not occur in peptide linkage in proteins; however, one residue per molecule is present in the peptide antibiotic telomycin. Residues of D-allothreonine have been found in the glycolipid and peptidolipid of actinomycetes, and in mycobacteria.



L-allothreonine D-allothreonine

allotopic **1** of, relating to, or having the property of **allotopy**. **2** *(in genetics)* describing a mutation that imparts to one tissue a particular metabolic characteristic normally found in another tissue.

allotopy the phenomenon of the formation of a membrane–enzyme complex resulting in alteration of the properties of both enzyme and membrane. For example, a change in enzymatic activity is sometimes observed when a soluble enzyme is adsorbed on an interface.

allotrope any of the different physical forms in which a chemical element can exist; e.g. diamond, graphite, and fullerenes are allotropes of carbon.

allotropy *or* **allotrophy** *or* **allotropism** the phenomenon of a substance, especially an element, existing in more than one physical form (**allotrope**), usually in the same phase; e.g. the different crystalline forms of carbon or phosphorus, or the different molecular forms of dioxygen and ozone. *Compare* **polymorphism** (def. 2). —**allotropic** *adj*.

allotype an antigenically distinct variant of a protein or other antigen arising from intraspecies genetic differences. Each individual has a particular variant at each immunoglobulin gene locus, which will often differ from those in other individuals of the same species.

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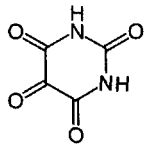
allotypic specificity an antigenic specificity that is not the same in a given protein in all normal individuals of a species.

allotypy the property, possessed by certain proteins and other antigens, of existing in antigenically distinct forms or **allotypes**. Thus allotypes of the same protein, although not distinguished by usual physicochemical and chemical criteria, can elicit specific antibodies in some other members of the same species. They are those **idiotypes** that behave as **xenotypes** in other individuals of the same species.

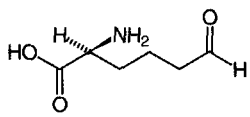
alloxan mesoxalylurea; 2,4,5,6-(1*H*,3*H*)-pyrimidinetetrone; a compound used experimentally to induce diabetes through its action in selectively destroying pancreatic B-cells.



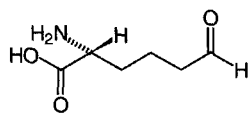
allozyme any enzyme variant produced by a particular **allele**.

allulose *trivial name (not recommended) for* **psicose**.

allysine 6-oxonorleucine; 2-aminoadipaldehydic acid; an α-amino acid not normally found in proteins but enzymically formed from lysine *in situ* as an intermediate in the creation of covalent cross-links between adjacent polypeptide strands during the maturation of certain connective-tissue proteins (e.g. collagen, elastin). The enzyme **lysyl oxidase** oxidizes the terminal amino-methylene groups of residues of either lysine or 5-hydroxylysine to aldehyde groups, forming residues of allysine or **hydroxyallysine** respectively. *See also* **desmosine**, **isodesmosine**, **lathyrism**, **noncoded amino acid**, **syndesine**.



L-allysine



D-allysine

almond emulsin *see* **1,3-α-L-fucosidase**.

ALP *(in clinical biochemistry) abbr. for* alkaline phosphatase.

alpha *symbol*: α (lower case) *or* A (upper case); the first letter of the Greek alphabet. For uses *see* **Appendix A**.

alpha cell *an alternative term for* **A cell**.

alpha-1 cell *an alternative term for* **D cell**.

alpha chain *or* **α chain** **1** the **heavy chain** of IgA **immunoglobulin** molecules. **2** one of the two types of polypeptide chain present in normal adult hemoglobin (Hb A) molecules.

alpha effect the enhancement of nucleophilicity that occurs when the atom adjacent to a nucleophilic site bears a lone pair of electrons. It has been invoked to explain the high toxicity of, e.g., hydroxylamine and the cyanide ion.

alpha-fetoprotein *see* **α-fetoprotein**.

alpha globulin *or* **α-globulin** any of a group of **plasma proteins** that migrate most anodically among the globulins in electrophoresis at pH values slightly above 7.

alpha helix *or* **α-helix** a helical, or spiral, configuration of a polypeptide chain in which successive turns of the helix are held together by hydrogen bonds between the amide (peptide) links, the carbonyl group of any given residue being hydrogen-bonded to the imino group of the third residue behind it in the chain. This is the case for all of the carbonyl and amide groups of the peptide bonds of the main chain. The alpha helix has 3.6 residues per turn and the **translation** (def. 2), or pitch, along the helical axis is 1.5 Å per residue and 5.4 Å per turn. The helix may be left- or right-handed, the latter being much more common. It is one of the two basic elements of the **secondary structure** adopted by a polypeptide chain within the hydrophobic core of a globular protein (the other being **beta strand**). The alpha helix was first described by **Pauling** and Corey in 1951, based on model building. *See also* **gamma helix**.

alpha hemolysis *or* **α-hemolysis** a type of hemolysis, characterizing certain strains of streptococci, in which a greenish tinge occurs around the bacterial colonies in a blood-agar plate. *Compare* **beta hemolysis**.

alphanumeric describing any coding system or data set that provides for letters, numbers, and other symbols such as punctuation. [From 'alphabetic' and 'numeric'.]

alpha oxidation *or* **α-oxidation** *a series of reactions occurring* in plant tissue by which a free fatty acid of chain length ranging from C_{18} to C_{13} is oxidatively degraded with the simultaneous release of a molecule of CO_2 from the carboxyl group and the formation of a free fatty acid containing one carbon atom fewer. NAD^+ is the only cofactor required.

alpha particle *or* **α particle** a fast-moving positively charged helium nucleus, $^4He^{2+}$, emitted in the decay of certain **radionuclides**.

alpha radiation radiation consisting of fast-moving alpha particles.

alpha ray a directed stream of alpha particles.

alpha receptor *see* **adrenoceptor**.

ALS *abbr. for* **1** antilymphocyte serum. **2** *(in clinical biochemistry)* (fructose-bisphosphate) aldolase, EC 4.1.2.13.

Alt *symbol for* altrose.

ALT *(in clinical biochemistry) abbr. for* alanine transaminase.

alternate pathway *see* **alternative pathway** (def. 2).

alternating axis of symmetry *see* **symmetry**.

alternating current *abbr.*: a.c. *or* AC; an electric current that varies with time in a sinusoidal manner. The abbreviation a.c. may also be applied to a voltage of varying polarity.

alternative pathway **1** a misleading term sometimes applied to any of the metabolic pathways by which glucose is broken down in animals, especially the **pentose (phosphate) pathway**. **2** (*or* **alternate pathway**) a pathway by which **complement** components C3–C9 are activated without a requirement for C1, C2, or C4.

alternative splicing the occurrence of alternative patterns of **splicing** of a primary RNA transcript of DNA to produce different mRNAs. After excision of **introns**, selection may determine which **exons** are spliced together to form the mRNA. An example is the production of mRNA for 19S IgM, which is secreted, and 7S IgM, which is inserted into the lymphocyte membrane, both products being coded for by the same gene, but the mRNA for 7S IgM having fewer of the original exons.

Altman, Sidney (1939–), Canadian-born US biochemist; Nobel Laureate in Chemistry (1989) jointly with T. R. Cech 'for their discovery of catalytic properties of RNA'.

altro- *prefix* denoting a particular configuration of a set of four (usually) contiguous >CHOH groups, as in D- or L-altrose. *See* **monosaccharide**.

altrose *symbol*: Alt; *altro*-hexose; an aldohexose that differs from glucose in the configuration of the hydroxyl groups on C-2 and C-3.

alum-precipitated toxoid any preparation in which a toxoid is adsorbed onto an adjuvant containing an aluminium compound, e.g. aluminium hydroxide gel or an alum. The term is applied especially to diphtheria toxoid.

alum precipitation a technique in which a soluble immunogen is converted into particulate form by mixing with a solution of

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an alum (e.g. aluminium potassium sulfate) and adjusting the pH to near 6.5. The antigen is adsorbed on the aluminium hydroxide precipitate so formed, which acts as an adjuvant in immunization.

Alu sequence *or* ***Alu*I sequence** *or* **Alu repeat** *or* ***Alu*I repeat** any of various base sequences dispersed in human, rat, and mouse (and perhaps other) genomes of ≈0.3 kbp and spaced at approximately 5 kbp. Each Alu sequence comprises two similar 130 bp boxes (**Alu left** and **Alu right**). The name derives from the presence in such sequences of sites for the restriction enzyme *Alu*I.

alveolus (*pl.* **alveoli**) any small pit, cavity, or saclike dilatation, such as an air cell of the lungs, an **acinus** of a compound gland, or a tooth socket. —**alveolar** *adj.*

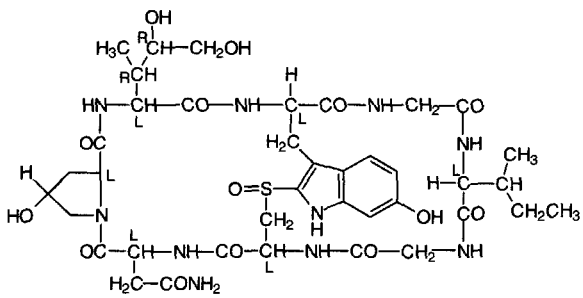
Alzheimer's disease *or* **Alzheimer's dementia** *or* **Alzheimer sclerosis** a genetically and phenotypically complex syndrome of progressive cognitive failure. It is the most common cause of late-life dementia (senile dementia) in developed nations, but early onset before the age of 65 (presenile dementia) may also occur. All cases develop numerous extracellular deposits of the **β-amyloid peptide** in the brain, and almost all have intraneuronal bundles of abnormal filaments composed of highly phosphorylated forms of the microtubule-associated **tau protein**. Missense mutations in the chromosome 21 gene coding for the β-amyloid peptide precursor have been described, and a chromosome 14q gene coding for a 467-amino-acid protein with seven putative membrane-spanning domains has been linked with the early-onset disease. Inheritance of the E_4 allele of the gene encoding **apolipoprotein E** is one of the main risk factors for late-onset Alzheimer's disease. [After Alois Alzheimer (1864–1915), German neurologist who in 1907 described the condition of a patient referred to as Auguste D.]

Am *symbol for* americium.

Amadori rearrangement an acid- or base-catalysed chemical rearrangement reaction in which an *N*-substituted aldosylamine is converted into the corresponding *N*-substituted 1-amino-1-deoxy-2-ketose. It occurs, e.g., in the **Maillard reaction**, in the reaction of carbohydrates with phenylhydrazine, in the formation of hemoglobin $A1_c$, and in a step in tryptophan biosynthesis – isomerization of *N*-(5′-phosphoribosyl)-anthranilic acid into 1-(α-carboxyphenylamino)-1′-deoxyribulose-5′-phosphate.

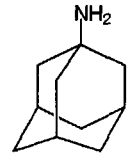
***Amanita* toxin** *see* **amatoxin**.

amanitin any of various **amatoxins**, especially α-, β-, γ-, and ε-amanitin. These occur, together with other **amatoxins**, in the highly poisonous agaric commonly called the death-cap fungus or deadly agaric (*Amanita phalloides*), and in some related species.



α-amanitin

amantadine *trivial name for* 1-adamantanamine; 1-aminoadamantane; $C_{10}H_{17}N$; a polycyclic antiviral agent that is especially effective as a prophylactic against influenza A virus. It appears not to affect viral attachment to cells but to block penetration or uncoating. *See also* **adamantane**.



amantadine

amatoxin any member of a family of closely related bicyclic octapeptides present in the highly poisonous agaric commonly called the death-cap fungus or deadly agaric (*Amanita phalloides*), and in some related species. α-**Amanitin** is the best known member and the chief toxic constituent of *A. phalloides*. The majority of amatoxins are highly toxic, though much slower in action than the congeneric and less potent phallotoxins. For example, the ingestion by an adult man of 10 mg α-amanitin (the quantity in a single fruit body of *A. phalloides*) leads over the course of several days to death in the absence of treatment. The common elements of the molecular structure of amatoxins include residues of *trans*-4-hydroxy-L-proline, (usually mono- or dihydroxy-)L-isoleucine, and the bisfunctional amino acid (usually 6′-hydroxy-)L,L-tryptathionine *S*-oxide (which forms a sulfoxide bridge across the molecule; *see* structure at **amanitin**), together with two residues of glycine. α-Amanitin binds very tightly ($K_{diss} = 10^{-8}$ M) to eukaryotic RNA polymerase II, thereby blocking the formation of mRNA precursors and hnRNA. It also binds, but rather less tightly ($K_{diss} = 10^{-6}$ M), to eukaryotic RNA polymerase III, thereby blocking the formation of tRNA and 5S RNA. It has little action on RNA polymerase I. Hence the synthesis of RNA and protein is markedly inhibited in eukaryotic cells but not in prokaryotic cells.

amber 1 a fossil resin. 2 *see* **amber mutant**.

amber codon *or* **amber triplet** *symbol*: UAG; one of the three terminator codons or **nonsense codons** in an mRNA molecule.

Amberlite *proprietary name for* various cation- and anion-exchange resins.

amber mutant *or* **amber** a T4 bacteriophage carrying an **amber mutation**. *See also* **ochre mutant**, **opal mutant**.

amber mutation a temperature-sensitive conditionally lethal mutation, capable of occurring in almost any gene of a bacterial virus, that causes the synthesis of a particular polypeptide chain to terminate prematurely. It is due to the alteration of one codon in the corresponding messenger RNA to an **amber codon**, i.e. a termination codon.

amber suppressor any of a number of mutations in *Escherichia coli* that suppress an **amber codon** in mRNA thereby allowing insertion of one of several alternative amino acids into a polypeptide at that site. The mutations result in changed anticodons of the tRNA molecules, consequent on single base substitutions in their DNA coding sequences.

ambi+ *or* **ambo+** *comb. form* denoting on both sides, both. *Compare* **amphi+**. [From Latin *ambo*, both.]

ambient of or relating to the immediate environment.

ambiquitous describing an enzyme that has reversibly convertible soluble and membrane-bound forms. —**ambiquity** *n.*

ambo+ *a variant form of* **ambi+**.

ambo- *prefix* designating chiral compounds in which both of the possible molecular configurations are present at an indicated chiral centre or residue but not necessarily in equimolar proportions. Such situations may arise especially with chiral compounds obtained by partial chemical synthesis from chiral precursors in asymmetric reactions. Examples: the amino-acid sequence Phe-*ambo*-Ala-Leu, representing a mixture of Phe-Ala-Leu and Phe-D-Ala-Leu; and the trivial name 4′-*ambo*-8′-*ambo*-α-tocopherol, representing a synthetic α-tocopherol in which C-2 has the natural, (*R*)-, configuration and C-4′ and

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C-8′ have both (*R*)- and (*S*)-configurations though not necessarily in equimolar proportions. *Compare* **DL-**, ***rac-***.

amboceptor *(formerly) an alternative term for* hemolytic antibody. [Named by Ehrlich, who pictured hemolysin as an antibody having specific receptors both for erythrocytes and for complement, thereby serving to link the two together.]

ameba *an alternative US spelling of* **amoeba**.

amelogenin the predominant protein in dental enamel during early development. Example (bovine): database code AMEG_BOVIN, 170 amino acids (19.24 kDa).

amidorphin an opioid peptide corresponding to residues 104–129 of bovine proenkephalin A, but which is amidated at its C terminus.

Ames test *see* ***Salmonella*** **mutagenesis test**.

amethopterin *another name for* **methotrexate**.

amidase EC 3.5.1.4; acylamide amidohydrolase; an enzyme that catalyses the hydrolysis of a monocarboxylic acid amide to monocarboxylate and NH_3.

ω-amidase EC 3.5.1.3; ω-aminodicarboxylate amidohydrolase; an enzyme that catalyses the hydrolysis of an ω-amidodicarboxylic acid to dicarboxylate and NH_3.

amidate to convert any oxy acid into its corresponding amide. —**amidated** *adj.*; **amidation** *n*.

amide any compound containing one, two, or three acyl groups attached to a nitrogen atom. An amide may be derived formally or actually by condensation of an oxy acid with ammonia or a primary or secondary amine. Amides derived from carbon acids may be termed **carboxamides**, those from sulfonic acids **sulfonamides**, etc. Examples include: acetamide, methanamide, $CH_3–CO–NH_2$; sulfanilamide, 4-aminobenzenesulfonamide, $H_2N–C_6H_4–SO_2–NH_2$; and diethylformamide, formdiethylamide, $H–CO–N(C_2H_5)_2$. The term includes **imide** and **peptide**.

amidination the process or reaction of introducing an amidino group into a chemical entity.

amidine any compound of the type $R–C(=NH)–NH_2$.

amidino the monovalent group $–C(=NH)–NH_2$.

amidino+ *comb. form* denoting the presence of an **amidino** group.

***N*-amidinoglycine** *see* **glycocyamine**.

amido+ *comb. form* denoting the presence of an amide group.

Amido Black *see* **Naphthalene Black**.

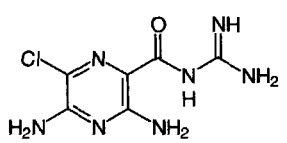
amidolysis any cleavage of an amide (including a peptide) to the parent oxy acid and ammonia or an amine.

amidophosphoribosyltransferase EC 2.4.2.14; *systematic name*: 5-phosphoribosylamine:pyrophosphate phospho-α-D-ribosyltransferase (glutamate-amidating); *other names*: glutamine phosphoribosylpyrophosphate amidotransferase; phosphoribosyldiphosphate 5-amidotransferase. An enzyme that catalyses the formation of 5-phospho-β-D-ribosylamine from L-glutamine, 5-phospho-α-D-ribose 1-diphosphate, and H_2O with release of L-glutamate and pyrophosphate. This is an early reaction in purine biosynthesis. Example from *Escherichia coli*: database code PUR1_ECOLI, 504 amino acids (56.38 kDa).

amidorphin an opioid peptide corresponding to residues 104–129 of bovine **proenkephalin** A, but which is amidated at its C terminus.

amidotransferase *see* **amidophosphoribosyltransferase**, **glutamine amidotransferase**.

amiloride *N*-amidino-3,5-diamino-6-chloropyrazinecarboxamide; a potent and specific inhibitor of Na^+ entry into cells. It inhibits Na^+,K^+-ATPase at low concentrations. It is used as a potassium-sparing diuretic.



amiloride-binding protein *see* **amine oxidase (copper-containing)**.

amine any organic compound that is weakly basic in character and contains an **amino** or a substituted amino group. Amines are called primary, secondary, or tertiary according to whether one, two, or three carbon atoms are attached to the nitrogen atom. *See also* **quaternary ammonium compound**.

amine oxidase (copper-containing) EC 1.4.3.6; *other names*: diamine oxidase; diamino oxhydrase; histaminase; an enzyme that catalyses the oxidation by dioxygen of an amino group to an aldehyde, with release of ammonium and hydrogen peroxide. 6-Hydroxydopa and copper are cofactors. Example, human amiloride-sensitive amine oxidase (copper-containing) precursor (amiloride-binding protein; *abbr.*: ABP): database code ABP_HUMAN, 751 amino acids (85.27 kDa); this enzyme binds **amiloride**.

amine oxidase (flavin-containing) *see* **monoamine oxidase**.

aminergic describing a receptor that is activated by a specific (biogenic) amine. The term is usually applied to nerves that act by releasing a monoamine (norepinephrine, dopamine, or 5-hydroxytryptamine) from their nerve endings. *Compare* **adrenergic**, **cholinergic**, **dopaminergic**, **peptidergic**, **purinergic**, **serotonergic**.

amino the chemical group $–NH_2$ in an organic molecule. It is basic in character and formally derived by the removal of a hydrogen atom from ammonia.

amino+ *comb. form* denoting the presence of an amino group.

amino acid any organic acid containing one or more amino substituents. The term is usually restricted to amino, especially α-amino, derivatives of aliphatic carboxylic acids, but it can also include β-amino derivatives.

amino-acid accepting RNA *see* **transfer RNA**.

amino-acid *N*-acetyltransferase EC 2.3.1.1; *other name*: *N*-acetylglutamate synthase (*abbr.*: AGS); an enzyme that catalyses the formation of *N*-acetyl-L-glutamate (*abbr.*: AGA) from acetyl-CoA and L-glutamate with the release of CoA. This is the enzyme responsible for the formation of AGA as an obligate activator of **carbamoyl-phosphate synthase** (def. 1), the first step in the **ornithine–urea cycle**. Example from *Escherichia coli*: database code ARGA_ECOLI, 443 amino acids (49.14 kDa). For another example, *see* **glutamate *N*-acetyl transferase**.

amino-acid analyser any instrument or apparatus for the automated analysis of mixtures of amino acids. The amino acids are separated individually and quantified spectrophotometrically.

amino-acid arm the base-paired segment of **transfer RNA** containing both the 3′ and the 5′ ends of the RNA molecule, on which the specific amino acid is attached to the 3′-hydroxyl at the 3′ end.

amino-acid oxidase any enzyme that catalyses the oxidation by dioxygen of the amino group of an α-amino acid to an oxo acid with release of ammonium and hydrogen peroxide. L-amino-acid oxidase, EC 1.4.3.2, is specific for L enantiomers and D-amino-acid oxidase, EC 1.4.3.3, is specific for D enantiomers. Both enzymes have FAD as coenzyme. Examples: L-amino-acid oxidase from *Neurospora crassa*: database code OXLA_NEUCR, 695 amino acids (76.80 kDa); D-amino acid oxidase (human) a peroxisomal enzyme: database code OXDA_HUMAN, 347 amino acids (39.37 kDa).

amino-acid residue that part of any amino-acid molecule that is present when the amino acid is combined in a (poly)peptide, i.e. the amino acid less the atoms (a hydrogen atom or/and a hydroxyl group) that have been removed during the formation of a peptide bond or bonds.

amino-acid sequence *or* **primary structure** the sequential order of amino-acid residues in a polypeptide or protein. It is usually given from the end carrying an α-amino group not in peptide linkage, i.e. from the N-terminal end.

amino-acid site *a less correct term for* **aminoacyl site**.

amino acid–tRNA ligase *other name*: aminoacyl-tRNA syn-

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thetase. Any of the sub-subclass EC 6.1.1 of enzymes that catalyse the formation of aminoacyl-tRNA from ATP, amino acid, and tRNA with release of pyrophosphate and AMP. Each amino acid has its cognate amino acid–tRNA ligase and tRNA acceptor species; e.g. in the case of glutamate–tRNA ligase (EC 6.1.1.17), the tRNA is $tRNA^{Glu}$ and the product is Glu-$tRNA^{Glu}$. The enzymes are complicated. Aminoacyl adenylate is normally an intermediate and the initial aminoacyl-tRNA product usually involves 2′-substitution with subsequent rearrangement. Specificity is not perfect but the enzymes have one or more mechanisms for correcting mischarged aminoacyl-tRNAs, which occur with structurally similar amino acids (e.g. Ile-$tRNA^{Val}$). Structurally the enzymes belong to several classes. Example of type I: tyrosine–tRNA ligase from *Bacillus stearothermophilus* (EC 6.1.1.1): homodimer, database code SYY_BACST, 419 amino acids (47.25 kDa). The 3-D structure of this, along with its mutants and complexes with substrates, is known; it has a large helical content and a characteristic ATP-binding motif.

amino aciduria a condition in which, on a normal dietary intake, amino acids appear in the urine. It may be due to renal defects or an inherited disease of amino-acid metabolism. *See* **Hartnup disease**, **maple syrup urine disease**.

aminoacyl the acyl group, R–CH(NH_2)–CO–, formed by removal of the hydroxyl group from the α-carboxyl group of an (unknown or unspecified) α-amino acid.

aminoacylase **1** EC 3.5.1.14; an *N*-acyl amino-acid aminohydrolase; an enzyme that catalyses any reaction of the general type:

N-acyl-L-amino acid (except *N*-acetylaspartate) + H_2O → fatty acid (anion) + amino acid.

Example (human): database code ACY1_HUMAN, 408 amino acids (45.88 kDa). **2** EC 3.5.1.15; *recommended name*: aspartoacylase; an enzyme that hydrolyses *N*-acetylaspartate to acetate and aspartate. Example (human): database code ACY2_HUMAN, 313 amino acids (35.73 kDa).

aminoacyl site *or* **A site** *or (correctly)* **aminoacyl-tRNA site** the site on a **ribosome** to which the incoming aminoacyl-tRNA is bound during protein synthesis. In bacteria this involves **ribosomal proteins** L1, L5, L7/L12, L20, L30, L33, both 16S and 23S rRNA (L7 and L12 differ in acetylation only).

aminoacyltransferase any enzyme of sub-subclass EC 2.3.2 that transfers aminoacyl groups, forming either an ester or an amide.

aminoacyl-tRNA the form in which amino acids are transported to the ribosomes during protein synthesis. The amino acid is esterified through its carboxyl group to the 3′-hydroxyl group of the 3′-terminal adenosine of a molecule of **transfer RNA**.

aminoacyl-tRNA synthetase *an alternative name for* **amino acid–tRNA ligase**.

α-aminoadipate 2-aminohexanedioate; an intermediate in the synthesis of lysine (*see* **aminoadipic pathway**). It is a competitive inhibitor of **glutamate receptors**.

aminoadipic pathway a metabolic pathway for the biosynthesis of lysine that occurs in some algae, *Euglena*, and fungi. It involves a two-carbon extension of 2-oxoglutarate to 2-oxoadipate (acetyl-CoA addition to form homocitrate, thence *cis*-homoaconitate, homoisocitrate, and oxidation to 2-oxoadipate), transamination to 2-aminoadipate, reaction of the latter with ATP to yield 5-adenylyl-2-aminoadipate, and further reductive reactions to 2-aminoadipic-5-semialdehyde, saccharopine, and finally L-lysine. Aminoadipate is also involved in lysine catabolism in mammals.

amino alcohol any aliphatic organic molecule or moiety containing both an amino and a hydroxyl substituent.

p-aminobenzoic acid *abbr.*: PABA; 4-aminobenzoic acid; a compound present in yeast as a factor in the B complex of vitamins, and a structural component of folic acid and related compounds. It is a substrate for the bacterial enzyme dihydropteroate synthase, EC 2.5.1.15, competitive inhibitors of which (e.g. **sulfonamides**) are effective antibacterial agents. It is used in sunscreen preparations. *De novo* synthesis is through the intermediate chorismate formed by the **shikimate pathway**. It is formed in a test of pancreatic function, the **PABA test**.

γ-aminobutyrate receptor *see* **GABA receptor**.

γ-aminobutyrate shunt *or* **GABA shunt** a variation of the **tricarboxylic-acid cycle** in which α-oxoglutarate is converted to L-glutamate either by transamination or by reductive amination. The glutamate is decarboxylated to form γ-aminobutyrate, which can re-enter the tricarboxylic-acid cycle after being oxidized to succinate. This metabolic pathway occurs in brain tissue, presumably to form γ-aminobutyric acid, and is also prominent in green plants.

4-aminobutyrate transaminase EC 2.6.1.19; *other names*: γ-amino-*N*-butyrate transaminase; GABA transaminase; β-alanine–oxoglutarate aminotransferase; an aminotransferase enzyme important in the metabolism of **γ-amino-*n*-butyric acid** (*abbr.*: GABA). It catalyses the reaction:

4-aminobutanoate (GABA) + 2-oxoglutarate = succinate semialdehyde + L-glutamate.

Example from yeast: database code GATA_YEAST, 471 amino acids (52.90 kDa).

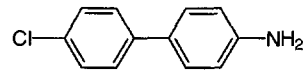
α-amino-*n*-butyric acid 2-aminobutanoic acid; a component of **ophthalmic acid**.

γ-amino-*n*-butyric acid *abbr.*: GABA; 4-aminobutanoic acid, H_2N–CH_2–CH_2–CH_2–COOH; an amino acid not found in proteins but occurring principally in the central nervous system, where it is an important inhibitory **neurotransmitter**. It is also found in some plants. *See also* **GABA receptor**.

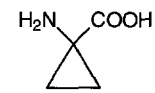
ε-aminocaproic acid *symbol*: εAcp; *(formerly) an alternative name for* **6-aminohexanoic acid**.

7-aminocephalosporanic acid a compound obtained by the acid hydrolysis of **cephalosporin** C and used in the manufacture of semisynthetic cephalosporins.

4-amino-4′-chlorodiphenyl *abbr.*: pCPA; an irreversible inhibitor of **tryptophan 5-hydroxylase** an enzyme in the pathway for synthesis of 5-hydroxytryptamine.



1-aminocyclopropane-1-carboxylic acid a key intermediate in the conversion of L-methionine into ethylene in higher plants. It is also a potent and selective ligand for the glycine modulatory site of the NMDA receptor (*see* **glutamate receptor**). It is formed from *S*-adenosyl-L-methionine by 1-aminocyclopropane-1-carboxylate synthase, EC 4.4.1.14.



aminodeoxysugar *or* **amino sugar** *or* **amino-saccharide** *or* **amino-monosaccharide** any monosaccharide or monosaccharide derivative in which an alcoholic hydroxyl group has been replaced by an amino group.

aminoethoxyvinylglycine *abbr.*: AVG; an inhibitor of ethylene formation in higher plants. It is produced by *Streptomyces* spp. It acts at the level of 1-aminocyclopropane-1-carboxylate synthase (*see* **1-aminocyclopropane-1-carboxylic acid**).

aminoethyl *symbol*: Aet; the –CH_2–CH_2–NH_2 group.

aminoethylbenzenesulfonyl fluoride *abbr.*: AEBSF; an inhibitor of serine endopeptidases. It is both soluble and stable in aqueous solutions, and is less toxic (LD_{50} 2.8 g kg^{-1}) than

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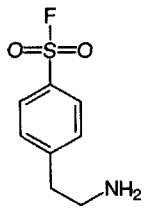
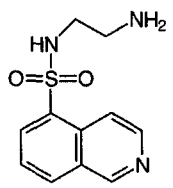
phenylmethylsulfonyl fluoride, but with the same action and similar potency. *Compare* **organophosphate**.



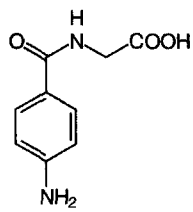
***N*-(2-aminoethyl)isoquinoline-5-sulfonamide** *or* **H9** a selective inhibitor of casein kinase I, protein kinase A, and, less potently, protein kinase C.



aminoglycoside antibiotic any member of a group of broad-spectrum antibiotics, of similar toxicity and pharmacology, that contain an aminodeoxysugar, an amino- or guanidino-substituted inositol ring, and one or more residues of other sugars. The group includes **streptomycin**, **neomycin**, framycetin, **kanamycin**, paromomycin, and **gentamicin**.

6-aminohexanoic acid *symbol*: εAhx; a compound that acts as an inhibitor of **streptokinase** and **urokinase** and prevents the synthesis of **plasmin**.

***para*-aminohippuric acid** *abbr.*: PAH; *N*-(4-aminobenzoyl)glycine; it is used in renal clearance tests. Its clearance exceeds that of inulin, indicating that it is actively secreted by renal tubular cells. It shares this transport system with penicillin and competitively inhibits penicillin secretion. PAH clearance is taken as a measure of effective renal plasma flow and the inulin:PAH clearance ratio as the filtration fraction, normally about 18%.



α-amino-3-hydroxy-5-methylisoxazolepropionic acid receptor *or* **AMPA receptor** an excitatory amino acid receptor coupled directly to a transmembrane cation channel. It was formerly known as the quisqualate receptor. It is a type of **glutamate receptor**.

aminoimidazole carboxamide ribonucleotide *see* **AICAR**.

aminoimidazole ribonucleotide *see* **AIR**.

amino–imino tautomerism a form of **tautomerism** in which the amino and the imino forms of a compound are in equilibrium, the change corresponding to the migration of a hydrogen atom. *Compare* **keto–enol tautomerism**.

α-aminoisobutyric acid α-methylalanine, 2-amino-2-methylpropanoic acid, $(CH_3)_2C(NH_2)COOH$; a non-metabolizable amino-acid analogue used in metabolic and other studies.

δ-aminolevulinate *or (esp. Brit.)* **δ-aminolaevulinate** *abbr.*: ALA, δALA, *or* DALA; 5-amino-4-oxopentanoate; $H_2N–CH_2–CO–[CH_2]_2–COO^-$; a compound formed in animals and bacteria from glycine and succinyl-CoA (*see* **5-aminolevulinate synthase**); in plant chloroplasts it is formed from glutamate (*see* **glutamate-1-semialdehyde 2,1-aminomutase**). It is an intermediate in **tetrapyrrole** biosynthesis.

5-aminolevulinate synthase EC 2.3.1.37; *systematic name*: succinyl-CoA:glycine *C*-succinyltransferase (decarboxylating); *other names*: δ-aminolevulinate synthase; δALA synthetase. The first and regulatory enzyme in the porphyrin biosynthetic pathway. It catalyses a reaction between succinyl-CoA and glycine to form 5-aminolevulinate, CoA, and CO_2. Pyridoxal phosphate is a cofactor. Example from human erythroid type (precursor): database code HEM0_HUMAN, 587 amino acids (64.62 kDa).

aminolysis **1** any chemical reaction in which an amine reacts analogously to ammonia in **ammonolysis**. **2** any hydrolytic deamination reaction in which an amino group is replaced by a hydroxyl group.

2-amino-4-methylhex-4-enoic acid a nonprotein amino acid found in plants, e.g. *Aesculus californica* (California buckeye).

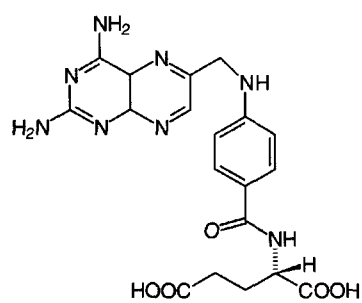
amino-monosaccharide *an alternative name for* **aminodeoxysugar**.

6-aminopenicillanic acid *abbr.*: 6-APA; a compound formally derived by the removal of the acyl side chain from **penicillin**. It is obtained industrially from fermentations in the absence of side-chain precursors but more usually by removal of the side chain using an amidase from *Escherichia coli* as an immobilized support. It is a very important intermediate for the manufacture of semisynthetic penicillins.

aminopeptidase any enzyme of sub-subclass EC 3.4.11, α-aminoacylpeptide hydrolases, that hydrolyse N-terminal amino-acid residues from oligopeptides or polypeptides.

4-aminophthalhydrazide *see* **luminol**.

aminopterin 4-aminofolic acid; a potent inhibitor of dihydrofolate reductase ($K_i < 10^{-9}$ M). It is used as an antineoplastic agent in the treatment of acute leukemia and choriocarcinoma. It blocks nucleotide biosynthesis and thus also DNA biosynthesis, and has a similar action to **amethopterin**.



amino-saccharide *an alternative name for* **aminodeoxysugar**.

amino-terminal determination the analysis of a peptide or a protein to determine the nature of the amino-acid residue at the N terminus. The free terminal α-amino group is substituted with a reagent such as 2,4-dinitrofluorobenzene (Sanger's reagent), dansyl chloride, or phenylisothiocyanate (Edman's reagent). The substituted terminal residue is then removed by hydrolysis and identified by, e.g., chromatography.

amino terminus *or* **amino terminal** *an alternative name for* **N terminus** (of a polypeptide chain when the α-amino, or α-imino group is free). *Compare* **carboxyl terminus**.

aminotransferase *or* **transaminase** any enzyme, of the large sub-subclass EC 2.6.1, that catalyses the reversible transfer of a nitrogenous group, usually an amino group, to an acceptor, generally a 2-oxo acid. Pyridoxal phosphate is a coenzyme, the

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intermediate pyridoxamine phosphate being formed in the reaction. *See also* **transamination**.

amitosis division of a cell nucleus by a process other than **mitosis**.

ammonification of nitrate *see* **nitrate reduction**.

ammonium **1** the NH_4^+ ion, formed by hydronation of a molecule of ammonia. It is formed from N_2 by root-nodule bacteria (*Rhizobium* spp.) in leguminous plants, and is an excretory product in **ammonotelic** animals. In higher animals it is toxic in elevated concentrations, and for excretion is converted to uric acid in **uricotelic** animals, and to urea in **ureotelic** animals. **2** the chemical group $-NH_3^+$.

ammonium sulfate $(NH_4)_2SO_4$; a salt much used in the purification of proteins, which vary in their solubility in ammonium sulfate solutions. An early step in the purification of a protein is thus often an ammonium sulfate precipitation.

ammonolysis any chemical reaction in which a covalent bond is cleaved by the action of ammonia, one or more of the hydrogen atoms of the ammonia being replaced by other atoms or groups; e.g.

$$2NH_3 + CH_3CO{-}O{-}COCH_3 \rightarrow CH_3CONH_2 + CH_3COO^-NH_4^+.$$

ammonotelic describing animal groups (e.g. crustaceans, marine mussels, octopods) in which ammonium is the principal end-product of the degradation of nitrogen-containing compounds.

amniocentesis the process of withdrawing a sample of amniotic fluid from the **amnion** by means of a hollow needle. It is particularly useful in the diagnosis of the status of a fetus with respect to proteins or DNA but, in the human, sampling can only be carried out during the second trimester of pregnancy.

amnion a membranous sac, filled with amniotic fluid, that surrounds and protects the embryo in higher animals. It is developed in reptiles, birds, and mammals but not in amphibians or fish.

amoeba *or (US)* **ameba** (*pl.* **amoebae** *or* **amebae**) any of a genus (*Amoeba*) of naked rhizopod protozoans in the order Amoebida, characterized by a thin pellicle and frequent alterations in shape due to the constant formation and retraction of pseudopodia. —**amoebic** *or (US)* **amebic** *adj.*

amoeboid *or (US)* **ameboid** **1** of, pertaining to, or reminiscent of an amoeba or amoebae. **2** describing cells, etc. that move by forming pseudopodia.

amorph a mutant allele that is inactive and fails to produce a measurable effect. It may act as a genetic block to normal biosynthesis.

amorphous **1** lacking definite shape or form. **2** noncrystalline; devoid of real or apparent crystalline form.

amount concentration *see* **concentration**.

amount of substance *or* **chemical amount** *symbol*: *n*; a fundamental physical quantity – one of the seven SI base physical quantities – proportional to the number of specified elementary entities of a substance (i.e. atoms, molecules, ions, radicals, electrons, etc., or any specified group(s) of such particles). The SI base unit of the amount of substance is the **mole**. The proportionality factor is the same for all substances, and is the reciprocal of the **Avogadro constant**, N_A. It is given by: $n_B = N_B/N_A$, where n_B and N_B are the amount of substance B and the number of entities of substance B, respectively. The terms 'amount of substance' and 'chemical amount' may often usefully be abbreviated to 'amount'.

amount-of-substance concentration *see* **concentration**.

amp *abbr. for* ampere.

AMP *abbr. for* adenosine monophosphate; i.e. adenosine phosphate.

2′AMP *abbr. for* adenosine 2′-monophosphate; i.e. adenosine 2′-phosphate.

3′AMP *abbr. for* adenosine 3′-monophosphate; i.e. adenosine 3′-phosphate.

5′AMP *abbr. for* adenosine 5′-monophosphate; i.e. adenosine 5′-phosphate.

AMPA receptor *abbr. for* DL-α-amino-3-hydroxy-5-methylisoxazolepropionic acid; *see* **α-amino-3-hydroxy-5-methylisoxazolepropionic acid receptor**.

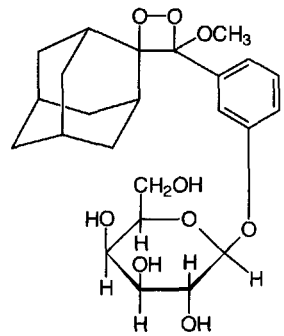
AMP-CP *abbr. for* 5′-adenylyl methylenephosphonate; i.e. adenosine 5′-[α,β-methylene]diphosphate.

AMP-CPP *abbr. for* 5′-adenylyl methylenediphosphate; i.e. adenosine 5′-[α,β-methylene]triphosphate.

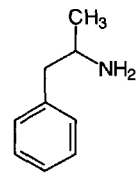
ampere *symbol*: A; *abbr.*: amp; the SI base unit of electric current. It is defined as that constant current, which if maintained in two straight parallel conductors of infinite length, of negligible circular cross-section, and placed 1 metre apart in a vacuum, would produce between these conductors a force equal to 2×10^{-7} newton per metre of length. [After André Marie Ampère (1775–1836), French physicist.]

amperometric titration any titration in which the end point is detected by measuring the electric current flowing when a potential is applied between two electrodes in a solution.

AMPGD *abbr. for* 3-(4-methoxyspiro)-1,2-dioxetane-3,2′-tricyclo[3.3.1.1]decan-(4-yl)phenyl-β-D-galactopyranoside; a chemiluminescent substrate for β-galactosidase (*see* **chemiluminescence**). It is used to detect the activity of the β-galactosidase gene when the latter is employed as a reporter gene in transgenic plants, etc.



amphetamine (*R,S*)1-phenyl-2-aminopropane; (±)-α-methylphenethylamine; racemic desoxynorephedrine; a drug that has potent effects by stimulating the release of monoamines, inhibiting **monoamine oxidase**, and blocking neuronal reuptake of monoamines from the synapse. It is noted for its marked CNS stimulant actions. *See also* **dextroamphetamine**.



amphi- *or (before a vowel)* **amph-** *prefix* **1** denoting on both sides of, of both kinds. **2** denoting around.

Amphibia a class of anamniote vertebrate animals in the superclass Tetrapoda. They are characterized by having gills during the larval stage; these are typically replaced by lungs in the adults. The skin is moist, glandular, and scaleless.

amphibian **1** a member of the class Amphibia. **2** adapted for life both on land and in water; amphibious.

amphibolic describing an enzyme or metabolic pathway that is concerned in both **anabolism** and **catabolism**. —**amphibolism** *n.*

amphile *an alternative name for* **amphiphile**.

amphion *or* **amphoion** any molecule that contains ionic groups of opposite charge, not necessarily in equal numbers; an ion-

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ized **ampholyte**. *Compare* **dipolar ion**. —**amphionic** *or* **amphoionic** *adj*.

amphipath *an alternative name for* **amphiphile**.

amphipathic *or* **amphiphilic** describing a molecule, such as a glycolipid or phospholipid, that contains both hydrophobic (i.e. lipophilic, nonpolar) and hydrophilic (i.e. aquaphilic, polar) parts; displaying **amphipathy**; being an **amphiphile**.

amphipathic helix an **alpha helix** with a specific topography consisting of opposite polar and nonpolar forces and a regular charge distribution. It is proposed as a basic structural element of the lipid-associating domains of apolipoproteins in very-low-density lipoproteins and high-density lipoproteins.

amphipathy *or* **amphiphilicity** the property (of a molecule, substance, etc.) of having affinity for both lipoidal and aqueous media; the extent or the degree to which a substance is amphipathic.

amphiphile *or* **amphile** *or* **amphipath** a substance whose molecules have an affinity for both aqueous and nonaqueous media; an **amphipathic** substance. [From Greek *amphi-*, of both kinds, + *philos*, loving.]

amphiphilic *an alternative term for* **amphipathic**.

amphiphysin an acidic protein that is localized in many synapses of avian and mammalian nervous systems and also expressed in adrenal gland and anterior and posterior pituitary tissues. It is an autoantigen in paraneoplastic stiff-man syndrome, a generalized progressive muscular hypertonia. Example from human: database code HSAMPHI, 695 amino acids (76.17 kDa).

amphiprotic describing a substance that can either gain or lose one or more protons.

amphiregulin a bifunctional transmembrane glycoprotein with a C-terminal EGF-like domain. It inhibits growth of several human carcinoma cells in culture and stimulates proliferation of human fibroblasts and certain other tumour cells. It is induced by phorbol acetate. Example from human: database code AMPR_HUMAN, 252 amino acids (27.86 kDa).

amphoion *a variant spelling of* **amphion**.

Ampholine *the proprietary name for* a series of mixtures of **carrier ampholytes**, which between them span the pH range 2.5–11. They consist of polyamino-polycarboxylic acids formed by reaction between acrylic acid and various polyethylene-polyamines. Each mixture contains a large number of ampholyte species of slightly differing isoelectric points. The mean and maximum apparent molecular masses are approximately 400 and 500 respectively. They are used in **isoelectric focusing**. They set up a pH gradient through the electrophoretic medium, and components being separated equilibrate to a point in the medium corrresponding to their isoelectric point.

ampholyte any amphoteric electrolyte; *see also* **carrier ampholyte**, **amphion**.

ampholyte-displacement chromatography a technique for the fractionation of protein mixtures by displacement chromatography on an ion exchanger using a mobile phase containing a mixture of amphoteric substances of closely spaced isoelectric points (i.e. carrier ampholytes). Separation of the components is thought to involve specific interaction between the proteins and the carrier ampholytes as well as competition between them for sites on the ion exchanger.

amphoteric describing a molecule that can react as acidic towards strong bases and as basic towards strong acids, e.g. an amino acid.

amphotericin B Fungizone; a polyene macrolide antifungal antibiotic produced by *Streptomyces* spp. It is useful against many mycotic infections, acting as a membrane-active lytic agent. At appropriate concentrations it permeabilizes cells, creating pores formed of five to ten molecules of antibiotic in association with cholesterol. These pores allow the passage of low M_r substances. Because it is active only against sterol-containing membranes, mitochondria are not affected. It interacts preferentially with ergosterol, giving it a high affinity for plant membranes; hence its value as a fungicide. *See also* **polyene antibiotic**.

ampicillin a semisynthetic antibiotic of the **penicillin** type, and having a $C_6H_5CH(NH_2)$– side chain.

ampicillin-resistant *symbol*: Ap^r; describing a cell, culture, organism, etc. that shows resistance to the lethal effects of the antibiotic **ampicillin**. This is a β-lactam antibiotic and resistance is often mediated by a class of enzymes called **β-lactamases**, which are secreted either into the periplasmic space of Gram-negative bacteria or into the medium of Gram-positive bacteria. The cloning vector pBR322 contains an ampicillin-resistance gene.

ampicillin-sensitive *symbol*: Ap^s; describing a cell, culture, organism, etc. that shows sensitivity to the antibiotic ampicillin.

amplification **1** the act, process, or result of amplifying. **2** the increase in the strength of an electromagnetic, chemical, or acoustic signal effected by an amplifier. **3** the production of additional copies of a stretch of genomic DNA, as a result of DNA either added to cells or originating in the chromosomes. These copies may result in tandem arrays in either an extrachromosomal or chromosomal location. This can result during selection of cells for resistance to certain agents; e.g. methotrexate blocks folate metabolism and may lead to amplification of dihydrofolate reductase genes. **4** the increase in the amount of a DNA with a specific sequence resulting from the **polymerase chain reaction**.

amplifier **1** an electronic device used to increase the strength of an electromagnetic signal; especially such a device used to increase the strength of an acoustic signal. **2** a combination of a receptor and various enzymes used to increase the strength of a chemical signal, as in a **cascade sequence**.

amplify to enlarge or to increase in strength or effect, especially an electromagnetic, acoustic, or chemical signal.

amplimer the amplified product of a **polymerase chain reaction**.

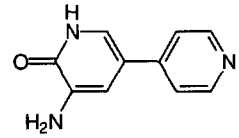
amplitude **1** magnitude; greatness of extent. **2** *symbol*: *a*; the maximal displacement from zero or from a mean position of an oscillation or a curve.

AMP-PCP *abbr. for* 5′-adenylyl methylenediphosphonate; i.e. adenosine 5′-[β,γ-methylene]triphosphate.

AMP-PNP *abbr. for* 5′-adenylyl imidodiphosphonate; i.e. adenosine 5′-[β,γ-imido]triphosphate.

AMP-S *abbr. for* adenosine 5′-[α-thio]monophosphate; i.e. adenosine 5′-thiophosphate.

amrinone 5-amino-(3,4′-bipyridin)-6(1*H*)-one; an inhibitor of cardiac (type III) phosphodiesterase, resulting in increased cardiac contractility and vasodilatation. It is useful in the treatment of heart failure.



AMS *(in clinical biochemistry) abbr. for* α-amylase.

amu *or* **AMU** *symbol for* atomic mass unit. *See also* **unified atomic mass unit**.

amunine *another name for* **corticotropin-releasing factor**.

amygdalin (–)-D-mandelonitrile β-D-gentiobioside; a **cyanogenic** glycoside derived biogenically from phenylalanine and found principally in oil of bitter almonds, although it is present in other plants belonging to the Rosaceae.

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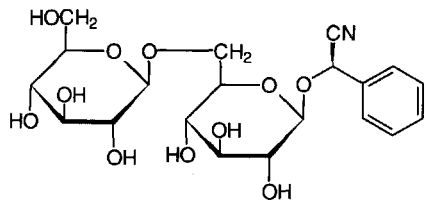


amygdalin

amygdalose *former name for* **gentiobiose**.

amyl *former name for* the **pentyl** group.

amyl+ *see* **amylo+**.

amylase any enzyme able to hydrolyse *O*-glucosyl linkages in starch, glycogen, and related polysaccharides (*see* **α-amylase**, **β-amylase**).

α-amylase EC 3.2.1.1; *systematic name*: 1,4-α-D-glucan glucohydrolase. An enzyme that catalyses the endohydrolysis of 1,4-α-D-glucosidic linkages with the production of mainly α-maltose from amylose, but also limit dextrins from **glycogen** and **amylopectin** since it cannot catalyse hydrolysis of 1,6 linkages. It is typical of animal cells (especially pancreas), and saliva. It has five motifs. The plasma level of α-amylase is raised in acute pancreatitis, and assay of the pancreas-specific isoenzyme aids diagnosis. Normal levels in human plasma are <300 IU L^{-1}, (this is very method-dependent). Example, α/β-amylase precursor from *Bacillus polymyxa*: database code AMYB_BACPO, 1196 amino acids (130.75 kDa). The protein is cleaved proteolytically to form the α (551 amino acids) and β (419 amino acids) enzymes.

β-amylase EC 3.2.1.2; *systematic name*: 1,4-α-D-glucan maltohydrolase; *other names*: saccharogen amylase; glycogenase. An enzyme that removes successive maltose units from the nonreducing ends of carbohydrate chains; the anomeric group undergoes inversion so that the major product is β-maltose. In some organisms it shares the same biosynthetic precursor as α-amylase. β-Amylases are characterized by their formation as insoluble zymogens during the process of seed maturation, and are also found in bacteria. Example from *Bacillus cereus* (precursor): database code AMYB_BACCE, 544 amino acids (61.33 kDa).

amylin *or* **islet amyloid polypeptide** (*abbr.*: IAPP) a 37-residue peptide, sequence KCNTATCATQRLANFLVHSSNNFG AILSSTNVGSNTY–NH_2, isolated from pancreatic islet amyloid deposits of an insulinoma and from amyloid-rich pancreases of type 2 diabetic patients; it is found in pancreatic cells and secreted with insulin. Structurally it closely resembles **calcitonin gene-related peptide** (CGRP), and has 43% and 46% amino-acid sequence homology with human α- and β-CGRP respectively. Like CGRP it is C-terminally amidated and has an N-terminal disulfide bridge linking cysteines 2 and 7. It opposes the action of glycogen synthase in skeletal muscle and may modulate insulin action. The peptide inhibits insulin-stimulated glucose metabolism in muscle but not in adipocytes. Example, human precursor: database code IAPP_HUMAN.

amylo+ *or (before a vowel)* **amyl+** *comb. form* denoting starch.

amylo-1,6-glucosidase EC 3.2.1.33; *other name*: dextrin 6-α-D-glucosidase; an enzyme that catalyses the endohydrolysis of 1,6-α-D-glucoside linkages at points of branching in chains of 1,4-linked α-D-glucose residues. Example (human) also has glycogen debranching enzyme (4-α-glucanotransferase) activity: database code GDE_HUMAN, 1515 amino acids (172.30 kDa).

amyloid **1** a waxy eosinophilic translucent material deposited in tissues in **amyloidosis**. Originally thought to be polysaccharide, it is now known to be fibrils made of protein molecules of various origins with a twisted β-pleated sheet structure. It is insoluble, and exhibits a green fluorescence when stained with Congo Red and viewed through crossed Nicol prisms. Amyloid fibres are relatively inert and resistant to solution in physiological solvents and to proteolytic enzymes. **2** pertaining to or characterized by the production of amyloid. **3** any non-nitrogenous substance resembling starch. **4** like or containing starch.

amyloid A protein *or* **serum amyloid A** (*abbr.*: SAA *or* AA) any of various plasma proteins synthesized by liver and induced by **cytokine** stimulation. The extracellular accumulation in various tissues of amyloid proteins results in secondary amyloidosis in human and other species. These deposits are highly insoluble and resistant to proteolysis. They disrupt tissue structure and compromise function. Four motifs are characteristic of SAAs. Example, SAA-1 (human) precursor: database code SAA1_HUMAN, 122 amino acids (13.43 kDa).

amyloidosis any of various pathological states in which the deposition of **amyloid** (def. 1) occurs in tissues. It is often associated with chronic infections and immunocyte dyscrasias. In the absence of medical intervention amyloid accumulates implacably, causing pressure atrophy of the affected tissue(s). Death subsequently results from interference with the normal physiological processes of affected vital organs. The descriptive term β-fibrillosis has been suggested for amyloidosis, after the beta-pleated sheet structure of the amyloid fibrils. However, the term is not commonly used. *See also* **amyloid A protein**.

β-amyloid peptide a glycoprotein associated with Alzheimer's disease and derived from a precursor, A4, capable of several forms through alternative splicing. It has three motifs. Database code (for human A4): A4_HUMAN, 770 amino acids (86.85 kDa).

amylolysis the process of converting starch into soluble oligo- and monosaccharides, especially by enzymic action. —**amylolytic** *adj.*

amylopectin a polydisperse highly branched **glucan** composed of chains of D-glucopyranose residues in α(1→4) glycosidic linkage. The chains are joined together by α(1→6) glycosidic linkages. A small number of α(1→3) glycosidic linkages and some 6-phosphate ester groups also may occur. The chains are of similar structure to those of glycogen but with fewer and longer branches. Those in amylopectin have been found variously to contain 24 to 30 glucose residues per nonreducing end-group. The size of the molecule varies greatly according to source and method of measurement, with average M_r values of 10^6 to 10^8 reported. Amylopectin occurs in starch, commonly as a mixture with about one-third its mass of **amylose**. However, some starches, notably the so-called waxy starch of maize (*Zea mays*), are almost pure amylopectin. Starch granules serve as the principal cellular store of glucose in most plants.

amylopectin 6-glucanohydrolase *see* **α-dextrin endo-1,6-α-glucosidase**.

amylopectinosis *see* **glycogen disease**.

amyloplast a colourless **plastid** or **leukoplast** in which starch is stored. It occurs in various plant tissues, e.g. cotyledons, endosperm, and storage organs such as potato tubers.

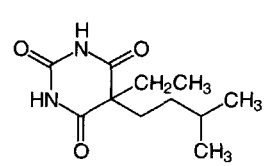
amylopsin *former term for* **pancreatic α-amylase**.

amylose a form of starch comprising a long unbranched **glucan** with α(1→4) glycosidic linkages.

amylosucrase *an alternative name for* **sucrase** (def. 3).

amylo-(1,4–1,6)-transglycosylase *see* **branching enzyme**.

Amytal *proprietary name for* the barbituric sedative 5-ethyl-5-isoamylbarbituric acid, 5-ethyl-5-isopentylbarbituric acid. It inhibits the **electron-transport chain** between flavoproteins and ubiquinone.



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an+ *or (before a consonant)* **a+** *prefix* indicating not, without.

+an *suffix* used in forming the semisystematic name of a parent chemical structure from the trivial name of the key compound to which the parent structure is related if the parent structure contains a heteroatom and is saturated e.g. glucosan, any internal anhydride of glucose.

An *symbol for* **anhydro+**.

anabiosis a return to life after apparent death; a state of suspended animation induced in an organism by, e.g., desiccation or freezing, and reversed by rehydration or warming.

anabolic pertaining to, involving, or exhibiting **anabolism**.

anabolic pathway any sequence of reactions involving **anabolism**; i.e. one in which energy is taken up. *Compare* **catabolic pathway**. *See also* **amphibolic**.

anabolic steroid any of various synthetic steroids that stimulate protein production *in vivo* by mimicking the action of **androgens**. Drug design aims to minimize masculinizing effects when used in female patients.

anabolism the energy-requiring part of metabolism in which simpler substances are transformed into more complex ones, as in growth and other biosynthetic processes. *Compare* **catabolism**.

anabolite any product of an **anabolic pathway**.

anabolize *or* **anabolise** to effect **anabolism**.

anaemia *a variant spelling (esp. Brit.) of* anemia.

anaerobe any organism that can grow in an atmosphere devoid of dioxygen. A **facultative anaerobe** is also capable of growing in a dioxygen-containing atmosphere whereas an **obligate anaerobe** (or strict anaerobe) can only grow in the absence of dioxygen.

anaerobic **1** describing an organism that is able to grow in the absence of dioxygen. **2** of or produced by an **anaerobe**. **3** (of an atmosphere) devoid of dioxygen. **4** (of a process) characterized by the absence of dioxygen.

anaerobic fermentation any of several catabolic pathways used by living organisms to extract chemical energy from various organic substances in the absence of dioxygen. *Compare* **anaerobic respiration**.

anaerobic glycolysis the metabolic pathways by which glucose is degraded anaerobically to lactate or ethanol. *See* **glycolysis**.

anaerobic indicator any indicator of the attainment and maintenance of anaerobic conditions in an **anaerobic jar**. It may be based on a dye that is decolorized in anaerobic conditions or consist of a culture of a strict anaerobe in one of the dishes in the jar.

anaerobic jar *or* **McIntosh & Fildes jar** an apparatus used to hold culture dishes or tubes under anaerobic conditions. It usually consists of an upright jar with an airtight lid; the air is evacuated and replaced by dihydrogen, which combines with any remaining dioxygen, the reaction being catalysed by a palladium catalyst. [After James McIntosh (1882–1948) and (Sir) Paul (Gordon) Fildes (1882–1971), British bacteriologists who first described the apparatus in 1916.]

anaerobic respiration the metabolic processes by which organisms degrade organic compounds in the absence of dioxygen to yield energy. They make use of inorganic oxidizing agents or accumulate reduced coenzymes. *Compare* **anaerobic fermentation**.

anaerobiosis life in the absence of dioxygen or air.

anagenesis the progressive or 'upward' evolution of a species; any evolutionary process that results in biological improvement. *Compare* **cladogenesis**. —**anagenetic** *adj.*; **anagenetically** *adv.*

anaglyph a stereoscopic moving or still picture made up of two superimposed images of the same object, taken from slightly different angles and reproduced in complementary colours (usually red and bluish green) so as to produce a three-dimensional effect when viewed through spectacles having one lens of each colour.

AnalaR *proprietary name for* any analytical (chemical) reagent that conforms to the tests and purity standards in *'AnalaR' Standards for Laboratory Chemicals* (1977) AnalaR Standards Ltd.

analbuminemia *or (esp. Brit.)* **analbuminaemia** a rare inherited disease in which there are very low plasma albumin levels but few symptoms.

analogous **1** having or showing similar or corresponding attributes. **2** *(in biology)* describing parts, organs, or tissues that have a similar function but differ in structure or evolutionary origin.

analogue *or (esp. US)* **analog** a chemical compound that is structurally similar to another. Such compounds can be used as probes to investigate specificity of, e.g. enzyme activity.

analogue enrichment *or* **analog enrichment** enrichment of microorganisms capable of co-metabolic degradation of organic pollutants by application of biodegradable analogues of the pollutant to the microbial ecosystem. *See* **co-metabolism**.

analyser *or (US)* **analyzer** **1** the **Nicol prism** of a polariscope or **polarimeter** that receives the light and indicates the degree and/or direction of rotation of its plane of polarization. *Compare* **polarizer**. **2** an instrument for routinely performing chemical analyses, often automatically and/or on a succession of samples. *See* **amino-acid analyser**, **autoanalyzer**, **sequenator**.

analysis (*pl.* **analyses**) **1** the process of determining the nature of the chemical constituents of a mixture or of the chemical groups present in a compound (**qualitative analysis**), or the process of determining the amounts of the constituents of a mixture (**quantitative analysis**). **2** the results of such an analysis. **3** the branch of mathematics concerned with the concepts of algebra and calculus. —**analytic** *or* **analytical** *adj.*

analysis of covariance a statistical method for determining the extent of the variance of one variable that is due to variability in some other variable.

analysis of variance a statistical method for segregating the experimentally observed variance between two populations into portions traceable to specific sources.

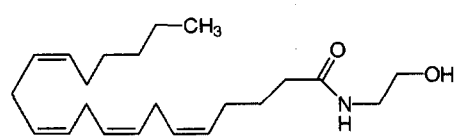
analyte a component to be measured in an **analysis** (def. 1).

analytical chemistry the branch of chemistry concerned with analysing materials by chemical (or physical) methods.

analytical ultracentrifuge an **ultracentrifuge** equipped with optical systems designed to determine concentration distributions at any time during the measurement. It is used in determinations of **sedimentation coefficients** and **sedimentation equilibrium**.

anamnestic reaction any immunological response in which a second or subsequent exposure to an antigen causes a greater and more rapid reaction than that elicited by the initial exposure. It is a manifestation of immunological memory.

anandamide arachidonoyl ethanolamide; a specific endogenous agonist that serves as a neurotransmitter of the **cannabinoid receptor**. It is formed in neurons by phosphodiesterase cleavage of *N*-arachidonoyl-phosphatidylethanolamine, and is probably then released to the extracellular space. A series of analogues such as *N*-linoleoyl ethanolamide and *N*-palmitoyl ethanolamide are formed simultaneously from appropriate precursors, but their role remains unclear. It may also be formed by condensation of arachidonate with ethanolamine. It is inactivated by reuptake into neurons and hydrolysis by *N*-acyl-ethanolamine amidohydrolase to ethanolamine and arachidonate.



anaphase a stage in **mitosis** or **meiosis** during which the two

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sister chromatids of each chromosome separate and move towards opposite poles of the spindle.

anaphylactic shock a severe generalized form of **anaphylaxis** in which there is widespread release of histamine and other vasoactive substances causing edema, constriction of the bronchioles, heart failure, circulatory collapse, and sometimes death.

anaphylactoid reaction an acute syndrome resembling **anaphylactic shock** though caused not by an immunological reaction but by injection of a variety of substances such as bee or snake venom.

anaphylatoxin any of a group of substances that mediate inflammation and are produced in serum during the fixation of **complement**, especially during the production of C3a and C5a. They cause mast cell degranulation and histamine release.

anaphylaxis extreme immunological sensitivity of the body or tissues to the reintroduction of an antigen. It is a form of **anamnestic reaction** and is accompanied by pathological changes in tissues or organs due to the release of pharmacologically active substances. —**anaphylactic** *adj.*

anaphylotoxin inactivator *see* **lysine(arginine) carboxypeptidase**.

anaplasia the reversion by a cell or tissue to a more primitive, embryonic, or undifferentiated form with loss of its characteristics and increased capacity for multiplication.

anaplerosis **1** the filling up of a deficiency; the repair or replacement of losses, especially of tissue. **2** *(in biochemistry)* the process in which an intermediate in a central metabolic pathway is replenished through a distinct **anaplerotic metabolic pathway**. This prevents the central pathway from ceasing to function because of withdrawal of the intermediate for some other metabolic purpose. [From Greek *ana*, again, back, up + *plerosin*, to fill.] —**anaplerotic** *adj.*

anaplerotic metabolic pathway any sequence of metabolic reactions that serves to maintain the operation of the central pathways of metabolism and which allows the operation and coordination of other metabolic pathways that enter and leave the central pathways.

anchorin CII *see* **annexin V**.

ancrod an enzyme, extractable from the venom of the Malayan pit viper, *Agkistrodon rhodostoma*, that produces unstable fibrin from fibrinogen by proteolysis. The resulting fibrinogen depletion results in an anticoagulant effect.

Andersen's disease *an alternative name for* type IV **glycogen disease**. [After Dorothy Hansine Andersen (1901–63), American physician.]

androgamone *see* **gamone**.

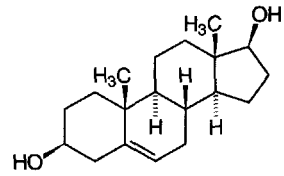
androgen any substance, natural or synthetic, that is able to stimulate the development of male sexual characteristics. Naturally occurring androgens are C_{19}-steroid hormones. They are produced especially by the testis (e.g. testosterone) and also by the adrenal cortex, ovary, and placenta. *Compare* **estrogen**. —**androgenic** *adj.*

androgen receptor any of the androgen-binding nuclear proteins that mediate the effects of androgens by regulating gene expression; they are **zinc-finger** proteins that bind discrete DNA sequences upstream of transcriptional start sites when the hormone–receptor complex is formed. The steroid-binding domain is in the C-terminal region. In humans, many variants are known that are associated with abnormalities, including testicular feminization syndrome, and complete or partial androgen insensitivity leading to external genitalia varying between female and nearly normal male. Example from human: database code ANDR_HUMAN, 919 amino acids (98.99 kDa).

androgen resistance *see* **testicular feminization**.

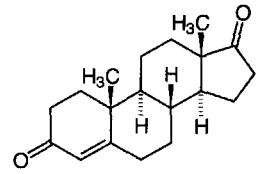
androstane the C_{19} parent compound from which androgens are structurally derived.

androstenediol 5-androstene-3β,17β-diol; a metabolite of dehydroepiandrosterone, from which it is formed by the action of 17β-hydroxysteroid dehydrogenase, EC 1.1.1.51.

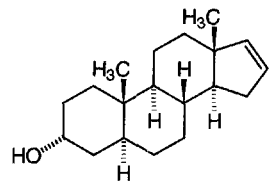


androstenediol

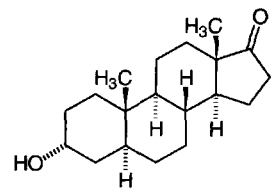
androstenedione 4-androstene-3,17-dione: a precursor of **testosterone** and **estrone**, formed in the testis and ovary from 17α-hydroxyprogesterone by the action of 17α-hydroxyprogesterone aldolase (17,20-lyase), EC 4.1.2.30, or from dehydroepiandrosterone by the action of 3β-hydroxy-Δ^5-steroid dehydrogenase, EC 1.1.1.145. It is also formed in adrenal cortex, from 17-hydroxypregnenolone by an isoenzyme of the 17,20-lyase. Androstenedione is secreted by the adrenals into the circulation and serves as a precursor for sex-hormone formation in peripheral tissues.



androst-16-en-3α-ol 3α-hydroxy-5α-androst-16-ene; 'boar taint'; a major constituent of boar pheromone. It is also present in truffles, which may account for the ability of pigs to locate these underground delicacies.



androsterone 5α-androstan-3α-ol-17-one; a metabolite of **testosterone**, from which it is formed in the liver via androstenedione. The latter is converted to androstanedione by 3-oxo-5α-steroid 4-dehydrogenase, EC 1.3.99.5. Androstanedione in turn is acted on by 3α-hydroxysteroid dehydrogenase, EC 1.1.1.213, forming androsterone.



+ane *suffix (in systematic chemical nomenclature)* denoting **1** an alkane, e.g. pentane. **2** a saturated heterocyclic compound in which the heteroatom is other than nitrogen, e.g. thiolane. **3 a** a hydride of boron, silicon, germanium, tin or lead, e.g. borane, silane; **b** a hydride of an unbranched chain of identical atoms of certain elements.

anemia *or (esp. Brit.)* **anaemia** any condition in which the blood has an abnormally low number of red cells (i.e. erythrocytes) or hemoglobin content, or is deficient in total volume.

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There are many causes, including hypersensitivity reactions to (e.g.) drugs (**hemolytic anemia**) and imbalance of Fe^{2+} metabolism (**iron deficiency anemia**). **Pernicious anemia** is characterized by defective production of erythrocytes and the presence of megaloblasts in the bone marrow; sometimes it is accompanied by neurological changes. It is caused by deficiency of vitamin B_{12} due either to a dietary deficiency of the vitamin or to a failure to produce **intrinsic factor** required for its absorption from the gut.

anergy *(in immunology)* any deficiency in the immune response to an agent that normally induces a response.

aneuploid describing a nucleus or organism in which the chromosome number is not an exact multiple of the haploid number (*n*). In humans (*n* = 23) examples include the presence of an extra copy of a single chromosome, e.g. trisomy 21 (Down's syndrome), or the absence of a single chromosome, e.g monosomy (as found in Turner's syndrome, 45,X). *Compare* **euploid**, **monosomic**, **nullisomic**, **trisomic**.

aneurin *or* **aneurine** *a former name for* **thiamine**.

Anfinsen, Christian Boehmer (1916–95), US protein chemist; Nobel Laureate in Chemistry (1972) 'for his work on ribonuclease, especially concerning the connection between the amino-acid sequence and the biologically active conformation' [prize shared with S. Moore and W. H. Stein].

angiogenesis the formation of blood vessels, whether during embryogenesis, tissue repair, or invasive growth of tumours.

angiogenin a **cytokine**, produced by fibroblasts, lymphocytes, and colon epithelial cells, that induces neovascularization and can serve as a substratum for endothelial and fibroblast cell adhesion. A monomeric protein, it is a member of the pancreatic ribonuclease family and specifically hydrolyses tRNAs, thus inhibiting protein synthesis. Example from *Mus musculus* (precursor): database code ANGI_MOUSE, 145 amino acids (16.23 kDa).

angiosperm a flowering plant; any member of the class Angiospermae, division Spermatophyta (seed plants). *Compare* **gymnosperm**.

angiotensin any of three related peptides, two of which regulate adrenal activity and also increase vasoconstriction and raise blood pressure. **Angiotensin I**, the decapeptide

H–Asp-Arg-Val-Tyr-Ile-His-Pro-Phe-His-Leu–OH,

is cleaved off **angiotensinogen** by the kidney enzyme **renin**; this peptide has no physiologically important action. **Angiotensin II**, the octapeptide formed from angiotensin I by removal of -His-Leu–OH by the action of **angiotensin converting enzyme**, is the most powerful pressor agent known, and the substance responsible for essential hypertension. It is also one of the most potent known stimulators of aldosterone production by the adrenal gland. It is rapidly destroyed by tissue peptidases, including **angiotensinase**. **Angiotensin III**, the heptapeptide formed by removal of the N-terminal Asp residue from angiotensin II (and the only one of its breakdown products to have activity), appears to be as active on the adrenal gland as angiotensin II and may also have significant vasoconstrictor activity.

angiotensinase an enzyme with proteinase activity that inactivates angiotensin II. Angiotensinase A is an alternative name for **glutamyl aminopeptidase**, EC 3.4.11.7, and angiotensinase C is another name for **lysosomal Pro-X carboxypeptidase**, EC 3.4.16.2.

angiotensin converting enzyme EC 3.4.15.1; *recommended name*: peptidyl dipeptidase A; *other names*: serum converting enzyme; peptidase P; peptidyl carboxypeptidase I; carboxycathepsin; kininase II. A Cl^--dependent zinc-containing dipeptidase present in lung, the brush borders of the proximal renal tubule, the endothelium of vascular beds, and plasma. It catalyses the release of a C-terminal dipeptide, -Xaa-|-Xbb-Xcc, when neither Xaa nor Xbb is proline, hence its conversion of angiotensin I to angiotensin II. It also acts on bradykinin. It is a transmembrane glycoprotein; two types (testis and somatic) arise by alternative splicing and different transcriptional start points. Example, somatic type precursor (human): database code ACE_HUMAN, 1306 amino acids (149.55 kDa).

angiotensin converting enzyme inhibitors compounds that prevent the synthesis of angiotensin II from its precursor, angiotensin I, e.g. **captopril**, **enalapril**. Such inhibitors are used in the treatment of cardiac failure and hypertension.

angiotensinogen a plasma α_2-globulin formed in liver and the precursor of **angiotensin** I, II, and III; it is similar to the **serpins**. Example, precursor from human: database code ANGT_HUMAN, 485 amino acids (53.09 kDa).

angiotensinogenase *see* **renin**.

angiotensin receptor any of several membrane proteins that bind angiotensin and mediate its intracellular effects. Two types of receptor, AT_1 and AT_2, have been identified on the basis of their response to drugs. The AT_1 receptor (previously known as AII_1 or AII_α) has high affinity for **losartan**, and lower affinity for CGP42112A; the reverse is true for AT_2 receptors. The potency of endogenous ligands is angiotensin II > angiotensin III. In peripheral tissues, AT_1 receptors, but not AT_2 receptors, interact with G-proteins, inhibit adenylate cyclase, and activate phospholipases C and A_2. AT_2 receptors may stimulate a phosphotyrosine phosphatase leading to inhibition of guanylate cyclase. Sulfhydryl reducing agents inhibit the binding of angiotensin II to AT_1 receptors but enhance its binding to AT. Both types are G-protein-coupled seven-transmembrane domain proteins. Examples: AT_1 receptor, database code AG2R_BOVIN, 359 amino acids (41.09 kDa); AT_2 receptor, database code AG22_MOUSE, 363 amino acids (41.37 kDa).

angle **1** the inclination between two lines or planes: **plane angle**. It is dimensionless and given in radians (*symbol*: rad), degrees (*symbol*: °; 1° = π/180 rad); minutes (*symbol*: ′) 1′ = π/10800 rad; or seconds (*symbol*: ″); 1″= π/64800 rad. **2** the (three-dimensional) vertex of a cone: **solid angle**. It is dimensionless but may be expressed in **steradians** (*symbol*: sr).

angle head *or* **angle rotor** any rotor for a centrifuge in which the tubes containing the liquid are at a fixed angle to the axis of rotation. *Compare* **swinging bucket rotor**.

ångström *or* **Ångstrom** *symbol*: Å; a unit of length equal to 10^{-10} metres. It is used in atomic measurements and for wavelengths of electromagnetic radiation, and is temporarily approved for use with SI units. [After Anders Jonas Ångström (1814–74), Swedish physicist noted for his work on spectroscopy.]

angular velocity *symbol*: ω; the rate of rotation of an object expressed as its rate of motion through an angle about an axis. It is expressed in rad s^{-1}.

anhydrase *see* **carbonic anhydrase**.

anhydride a derivative of a substance that yields the substance when combined chemically with water.

anhydro- *symbol*: An; *prefix* (in a chemical name) denoting the loss of the elements of water from within one molecule or residue. The positions from which removal has occurred may be indicated by a pair of locants, e.g. 2,5-anhydro-D-gluconic acid.

anhydrosialidase EC 3.2.1.138; *other names*: anhydroneuraminidase; sialidase L; an enzyme that catalyses the hydrolysis of α-sialosyl linkages in *N*-acetylneuraminic acid glycosides, releasing 2,7-anhydro-α-*N*-acetylneuraminic acid.

anhydrosugar any intramolecular ether formed by the elimination of water from two (indicated) alcoholic hydroxyl groups of a single molecule of a monosaccharide, whether aldose or ketose; i.e. any anhydromonosaccharide whose formation does not involve the reducing group.

anhydrous devoid of water, especially (of a substance or material) lacking water of crystallization or adsorbed water, or (of an environment) very dry. *See also* **dehydration**.

animal pole *see* **vegetal pole**.

animal protein factor a name formerly used for a growth factor for livestock, found to be present in meat and fish but not

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in feeds of plant origin. It was later shown to be identical with anti-pernicious anemia factor, i.e. vitamin B_{12}.

anion an **ion** with a net negative charge; during electrolysis of a solution anions migrate towards the **anode**. *Compare* **cation**. —**anionic** *adj*.

anion exchanger *or* **anion-exchange resin** any **ion-exchange resin** that carries positively charged groups, e.g. quaternary ammonium groups, and binds anions.

anion gap *(in clinical chemistry)*, the difference, in meq L^{-1}, between the concentrations of serum sodium plus potassium and of the serum chloride plus bicarbonate; i.e.

$$\text{anion gap} = [Na^+ + K^+] - [Cl^- + HCO_3^-].$$

Normal values are 12 ± 2 meq L^{-1}. Variations in the anion gap provide a useful insight into the acid–base status of a subject.

anionic detergent a detergent in which the polar part of the molecule carries a negative charge. *Compare* **nonionic detergent**.

anisotropic describing a medium in which physical properties, such as the velocity of electromagnetic radiation transmission, electrical or heat conductivities, or compressibility, have different values when measured along axes in different directions. —**anisotropically** *adv*.; **anisotropy** *or* **anisotropism** *n*.

anisotropic motion rotation about a single axis, especially of a molecule or a **spin label**.

ankyrin *or* **band 2.1 (protein)** *or* **nexin** *or* **syndein** a 200 kDa cytoskeletal protein that attaches other cytoskeletal proteins to integral membrane proteins. It is bound tightly to the cytoplasmic surface of the human erythrocyte membrane, to which it attaches the cytoskeletal protein **spectrin**. Example from human: database code ANK1_HUMAN, 1880 amino acids (206.14 kDa). [After the Greek *ankyra*, anchor].

annealing **1** the renaturation of heat-denatured nucleic acids or proteins by slow cooling. **2** the formation of hybrid double-stranded nucleic-acid molecules by the slow cooling of a mixture of denatured, single-stranded nucleic acids. It is used to detect complementary regions of different nucleic-acid molecules. **3** the slow regulated cooling, especially of metals or glasses, to relieve the stresses caused by heating or other treatments. —**annealer** *n*.

annexin any of a ubiquitous family of Ca^{2+}-dependent phospholipid-binding proteins. They have been isolated from organisms as diverse as mammals, *Drosophila melanogaster*, and *Hydra vulgaris*. Characteristically they have a low intrinsic affinity for Ca^{2+} (K_d 25–1000 μM), although annexin VI has $K_d \approx 1$ μM, but in the presence of phospholipid the affinity for Ca^{2+} increases up to 100-fold. The Ca^{2+}- and phospholipid-binding properties that typify the family derive from a region of common primary structure (identity with any other member of the family is 40–60%) in a conserved 34 kDa C-terminal region (the 'core'); each different type of annexin has a unique N-terminal domain known as the 'tail'. The C-terminal region in all cases except one consists of four repeats of a ≈70 amino-acid sequence, in which there is a high homology region known as the **endonexin fold**, with a characteristic motif GXGTDE; the exception is annexin VI, which has eight repeats. The true physiological roles of the annexins remain unknown, but their main characteristics, exhibited variously by different annexins and reflected in the alternative names they acquired in the course of discovery, include: the ability to aggregate membranes and vesicles (all annexins); inhibition of phospholipase A_2 (especially I, but also II to VI); formation of ion channels (especially I and V to VII); anticoagulant properties (especially I, and VIII); and acting as substrates for tyrosine kinases (I and II) and protein kinase C (I, II, IV, and XII). Alternative names and database codes are given under the individual entries.

annexin I *other names*: lipocortin I; p35 (EGF receptor substrate); calpactin II; chromobindin 9; GIF; lipomodulin; macrocortin; renocortin. Example from rat: database code ANX1_RAT, 345 amino acids (38.65 kDa).

annexin II *other names*: calpactin I heavy chain; lipocortin II; p36 ($pp60^{src}$ substrate); chromobindin 8; protein I; placental anticoagulant protein (PAP)-IV. Example from human: database code ANX2_HUMAN, 338 amino acids (38.43 kDa).

annexin III *other names*: lipocortin III; placental anticoagulant protein (PAP)-III; 35-α-calcimedin; calphobindin III; inositol 1,2-cyclic phosphate hydrolase. Example from rat: database code ANX3_RAT, 324 amino acids (36.28 kDa).

annexin IV *other names*: endonexin I; protein II; 32.5K calelectrin; lipocortin IV; chromobindin 4; placental anticoagulant protein (PAP)-II; placental protein PP4-X; 35-β-calcimedin; placental anticoagulant protein II. Example from human: database code ANX4_HUMAN, 318 amino acids (35.68 kDa).

annexin V *other names*: placental anticoagulant protein (PAP)-I; inhibitor of blood coagulation (IBC); lipocortin V; 35K calelectrin; endonexin II; placental protein PP4; vascular anticoagulant (VAC)-α; 35-γ-calcimedin; calphobindin I; anchorin CII. Example from human: database code ANX5_HUMAN, 319 amino acids (35.76 kDa).

annexin VI *other names*: p68; p70; 73K; 67K calelectrin; lipocortin VI; protein III; chromobindin 20; 67K calcimedin; calphobindin II; synhibin. Example from human: database code ANX6_HUMAN, 672 amino acids (75.66 kDa).

annexin VII *another name for* **synexin**.

annexin VIII *other name*: vascular anticoagulant (VAC)-β. Example from human: database code ANX8_HUMAN, 327 amino acids (36.84 kDa).

annexin IX *other name*: *Drosophila melanogaster* annexin. Database code (fragment) from *D. melanogaster*: ANX9_DROME.

annexin X *other name*: intestine-specific annexin. Example from human: database code ANXI_HUMAN, 315 amino acids (35.29 kDa). A similar protein occurs in *Drosophila melanogaster*.

annexin XI *other names*: (sometimes, e.g. in rabbit) calcyclin-associated annexin (CAP); CAP-50. There are two variants (derived by alternative splicing). Example, variant I, bovine: database code ANXA_BOVIN, 503 amino acids (53.96 kDa).

annexin XII a member of the annexin family obtained from *Hydra attenuata* (*Hydra vulgaris*). It is of unknown function. Example from *H. vulgaris*: database code ANXC_HYDAT, 316 amino acids (35.07 kDa).

annihilation radiation electromagnetic radiation of wavelength 2.4 pm (energy 0.51 MeV) that is emitted as a pair of photons when a positron absorbed into matter reaches the end of its range and combines with an electron in mutual destruction.

anode **1** the electrode of an electrolysis cell or electrophoresis apparatus towards which anions of the electrolyte migrate under the influence of an electric field applied between the electrodes. **2** the positive electrode, pole, or terminal of such a cell or apparatus, or of a discharge tube, solid-state rectifier, or thermionic valve; the electrode by which electrons flow out of the device. **3** the negative pole or terminal of an electric (primary or secondary) cell or battery (of cells). *Compare* **cathode**. —**anodal** *or* **anodic** *adj*; **anodally** *or* **anodically** *adv*.

anodic stripping voltammetry *abbr*.: ASV; an electrochemical procedure for estimating the concentration of metal ions in a solution. Exhaustive or partial (depending on the concentrations involved) deposition of the metal occurs on the cathode of an electrolytic cell at a constant applied electric potential (controlled potential deposition can be used for selectivity when mixtures are involved). The metal deposit is then anodically stripped by using a rapid sweep of voltage of opposite polarity and a peak-type current–voltage curve is obtained. The amount of metal deposited may be calculated coulometrically from the area under the peak, or by other means, and hence the concentration of metal ions in the initial solution may be determined.

anodic to during electrophoresis, migrating further towards

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the anode or less far towards the cathode than (the specified substance).

anolyte the electrolyte in immediate contact with the anode in isoelectric focusing.

anomalous dispersion **1** an X-ray crystallographic dispersion that occurs when the frequency of the X-rays used falls near an absorption frequency of an atom in the crystal. Anomalous dispersion techniques are frequently used in the determination of absolute configuration. **2** an optical rotatory dispersion that cannot be expressed by a simple one-term **Drude equation**.

anomer either of the two stereoisomers of the cyclic form of an **aldose** or a **ketose**, or an aldose or ketose derivative, dependent on the position of the free hydroxyl group belonging to the internal hemiacetal grouping. The anomer having the same configuration, in the **Fischer projection**, at the anomeric and the reference asymmetric carbon atom is designated α; the other anomer is designated β. In correct usage in regard to carbohydrates, the anomeric and configurational descriptors must always be linked together; e.g. α-D-glucopyranose, not α-glucose.

anomeric **1** of or pertaining to an **anomer**. **2** *or* **glycosidic** of or pertaining to the free hydroxyl group belonging to the internal hemiacetal grouping in the cyclic form of a monosaccharide or monosaccharide derivative.

anomeric effect the tendency for an electronegative substituent at C-1 of a pyranose to assume the axial orientation, in contrast to the equatorial orientation predicted on steric grounds.

anorexia absence of desire for food.

anosmia loss of the sense of smell.

anoxia the absence or a deficiency of dioxygen. *Compare* **hypoxia**. —**anoxic** *adj.*

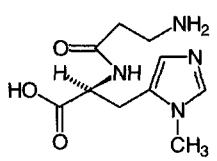
ANP *abbr. for* atrial natriuretic peptide. *See* **natriuretic peptide**.

ANPR *abbr. for* atrial natriuretic peptide receptor.

ANS *abbr. for* 1-anilino-8-naphthalene sulfonate; a common fluor used in extrinsic fluorescence studies of proteins.

ansamycin any antibiotic belonging to the **rifamycin** or the **streptovaricin** classes.

anserine *N*-β-alanyl-N^{π}-methyl-L-histidine; an isopeptide occurring in skeletal muscle and brain of some animals and humans (up to 20 mmol kg^{-1}). *Compare* **carnosine**.



Anson unit an old measure of the activity of a proteinase. It was based upon the extent to which a sample containing a particular proteinase can digest denatured hemoglobin, under standard conditions appropriate to the enzyme in question, with liberation of nonprecipitable material giving the same colour value as one millimole of tyrosine on reaction with a diluted Folin–Ciocalteau reagent. [After Mortimer Lewis Anson (1901–68), US protein chemist, who described it in 1958.]

ant+ *a variant of* **anti+**.

Antabuse *proprietary name for* **disulfiram**.

antagonism **1** opposition; counteraction. **2** the mutual opposition of an agonist and an antagonist. **3** the interference with, or inhibition of, the growth of an organism by one of another kind, as by competing for nutrients or producing an antibiotic substance.

antagonist **1** anything that antagonizes. **2** any agent, especially a drug or hormone, that reduces the action of another agent, the **agonist**. Many act at the same receptor as the agonist. Such antagonists may be either surmountable or insurmountable, depending on prevailing conditions. Antagonism may also result from combination with the substance being antagonized (**chemical antagonism**), or the production of an opposite effect through a different receptor (**functional antagonism** or **physiological antagonism**), or as a consequence of competition for the binding site of an intermediate that links receptor activation to the effect observed (indirect antagonism). The term 'functional antagonism' is also used to describe a less well-defined category in which the antagonist interferes with other events that follow receptor activation. **3** a muscle that works in opposition to another (the agonist). *See also* **competitive antagonism**, **noncompetitive antagonism**. *Compare* **agonist**, **inverse agonist**, **synergist**. —**antagonistic** *adj.*; **antagonistically** *adv.*

antagonize *or* **antagonise** to act in opposition to; to counteract. —**antagonized** *or* **antagonised** *adj.*

antanamide a highly lipophilic homodetic cyclic decapeptide, cyclo(-Pro-Phe-Phe-Val-Pro-Pro-Ala-Phe-Phe-Pro-). It occurs in the death-cap fungus, *Amanita phalloides*, together with the **amatoxins** and **phallotoxins**. When administered to experimental animals (at 1 mg per kg of body weight), either before or at most a few minutes after a lethal dose of phallotoxin, it acts as an antidote to the toxin, apparently by competing for binding sites. *In vitro* it readily forms complexes with sodium and calcium ions, and can act as a sodium ionophore.

ANT-C *abbr. for* antennapedia complex; one of two major families of homeotic genes of *Drosophila* (the other being **BX-C**), mutation which affects head and thoracic segments.

ante+ *prefix* denoting before in time or position.

antegrade *a variant of* **anterograde**.

anteiso+ *prefix* denoting a branched-chain fatty acid having a methyl group at the *n*-3 position; e.g. 16-methyloctadecanoic acid, also named anteisononadecanoic acid.

antenna complex any of the light-harvesting pigment-protein complexes of photosynthetic organisms that funnel absorbed incident radiation to the photochemical reaction centres.

antennapedia complex *see* **ANT-C**.

anterograde *or* **antegrade** **1** moving forwards; extending towards the front. **2** moving along the axon of a nerve cell in a direction away from the cell body (as in anterograde transport of vesicles). *Compare* **retrograde**.

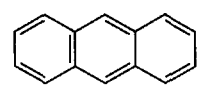
antheridiol a steroid hormone produced by water moulds (e.g. *Achyla* spp.) to regulate their sexual reproduction.

anthocyanidin any member of a group of water-insoluble red, blue, or violet polyhydroxylated 2-phenylbenzopyrylium compounds that occur as glycosides – anthocyanins – in plants. They comprise one class of the widespread group of flavonoids.

anthocyanin any member of a group of intensely coloured soluble glycosides of anthocyanidins that occur in plants. They are responsible for most of the scarlet, purple, mauve, and blue colouring in higher plants, especially of flowers.

antho-K amide L-3-phenyllactyl-Phe-Lys-Ala–NH_2; a neuropeptide from the sea anemone *Anthopleura elegantissima*.

anthracene a tricyclic aromatic compound, $C_{14}H_{10}$; it is a component of a number of **scintillation cocktails**.



anthralin 1,8-dihydroxyanthrone; a substance that inhibits **leukotriene** biosynthesis. It is used as an antipsoriatic drug.

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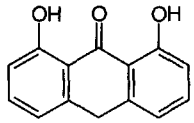
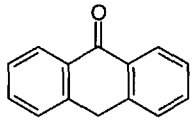


anthralin

anthranilate 2-aminobenzoate (anion, salt, or ester); an intermediate in the biosynthesis of tryptophan.

anthranilate synthase EC 4.1.3.27; *systematic name*: chorismate pyruvate-lyase (amino-accepting). An enzyme that catalyses the first step in tryptophan biosynthesis, in which chorismate and L-glutamine react to form anthranilate, pyruvate, and L-glutamate. It is a tetramer of two components, I and II: in the absence of II, I catalyses the formation of anthranilate using NH_3 rather than glutamine; II provides glutamine amidotransferase activity. Example from yeast: I database code TRPE_YEAST, 528 amino acids (59.70 kDa); II database code TRPG_YEAST, 484 amino acids (53.46 kDa).

anthrone 9(10*H*)-anthracenone; a compound used in the colorimetric determination of carbohydrates, especially hexoses, with which it gives a green colour.

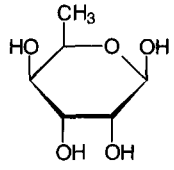


anti+ *or (sometimes before a vowel or h)* **ant+** *prefix* **1** acting against, counteracting, or inhibiting. **2** opposite to (in direction). **3** converse or reverse of; complementary to.

anti+ *prefix (obsolete)* denoting a *cis* isomer.

antiamoebin *or* **antiamebin** *see* **peptaibophol**.

antiarose the D isomer, 6-deoxy-D-gulose; occurs in glycosidic linkage in some **cardiac glycosides**.



β-D-pyranose form

antibiotic **1** any of numerous substances of relatively low M_r produced by living microorganisms (and also certain plants) that are able selectively and at low concentrations to destroy or inhibit the growth of other organisms, especially microorganisms. Also included are the many semi- or wholly synthetic organic compounds with similar antimicrobial properties. Many are useful chemotherapeutic agents. **2** of or relating to an antibiotic.

antibody any glycoprotein of the **immunoglobulin** family that is capable of combining noncovalently, reversibly, and in a specific manner with a corresponding antigen. Antibodies frequently, but not always, counteract the biological activity of antigens. They are produced in higher animals by cells of the lymphoid cell series, especially plasma cells, in direct response to the introduction of immunogens or autocoupling haptens. Antibodies were originally identified as a class of serum proteins, and most are present in the γ-globulin fraction of the serum. In the ultracentrifuge most antibodies have a sedimentation coefficient of 7S, except for the pentameric IgM at 19S. *See also* **cell-bound antibody**.

antibody-mediated hypersensitivity *or* **type II hypersensitivity** an immune response caused by the presence of antibody to cell-surface antigens and components of the extracellular matrix. These antibodies can sensitize the cells for antibody-dependent cytotoxic attack by **K cells** or **complement**-mediated lysis. Type II hypersensitivity is seen in the destruction of red cells in transfusion reactions and in hemolytic disease of the newborn.

anticholinesterase any agent, other than an antibody, that inhibits **cholinesterase** (def. 2). An example is **physostigmine**, used in the diagnosis and treatment of myasthenia gravis.

anticircular chromatography a technique of thin-layer chromatography in which the substances to be separated are applied just inside the perimeter of a circular thin-layer plate and are made to travel radially inwards by subsequent application of the developing solvent at the edge of the plate. It is very fast and is particularly useful for the resolution of substances whose R_f values approach unity. *Compare* **circular chromatography**.

anticlinal *see* **conformation** (def. 2).

anticoagulant **1** retarding or preventing coagulation. **2** any substance that retards or prevents coagulation, especially of blood or milk.

anticoagulate to treat (esp. blood) so as to prevent coagulation.

anticodon a triplet of nucleotides in any particular transfer RNA that is complementary to and therefore pairs with a given **codon** in messenger RNA. The pairing is antiparallel, 5′→3′ in the messenger, 3′→5′ in the anticodon. Thus the anticodon of 5′-ACG-3′ is 3′-UGC-5′. However, to maintain the convention of writing sequences in the 5′→3′ direction, the anticodon is thus written, but with a reverse arrow above: $\overleftarrow{\text{CGU}}$.

anticodon arm the part in the clover-leaf model of transfer RNA containing a loop bearing the anticodon.

anticooperativity negative **cooperativity** between binding sites on the same (macro)molecule by which binding of a ligand to one site makes the binding of a second ligand more difficult.

antidiuretic **1** describing any drug or other agent that decreases the excretion of urine. **2** an antidiuretic substance.

antidiuretic hormone *abbr.*: ADH; *an alternative name (esp. in clinical chemistry) for* **vasopressin**. It is so named from the hormone's most important biological action, viz. reduction of the rate of urine output by stimulation of the rate of water reabsorption by the kidney(s).

antidote a substance or other agent that limits or reverses the effects of a poison.

antifolate any of a class of drugs that interfere with the formation of tetrahydrofolate, and are used in the treatment of acute leukemia and choriocarcinoma. One of the best known is **methotrexate**.

antifreeze glycoprotein any of a group of glycoproteins found in the serum of certain cold-water fish, particularly notothanids and chaenichthyids, which inhabit polar seas; e.g. *Trematomus borchgrevinki* and *Dissostichus mawsoni*. These glycoproteins depress the freezing point of aqueous solutions about 200–500 times as effectively as sodium chloride on a molar basis. They differ only in mass (10.5 kDa, 17 kDa, and 21.5 kDa) and are composed of repeating units of a diglycosyl tripeptide, Ala-Ala-Thr-*O*-disaccharide, in which the disaccharide consists of a *β*-galactosyl residue bound to an internal *α*-*N*-acetylgalactosaminyl residue.

antigen **1** (*or* **complete antigen**) any agent that, when introduced into an immunocompetent animal, stimulates the production of a specific antibody or antibodies that can combine with the antigen. It may be a pure substance, a mixture of substances, or particulate material (including cells or cell fragments). In this sense the term includes **agglutinogen** and

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allergen and is synonymous with **immunogen** (def. 1). **2** (*or* **incomplete antigen**) any substance that can combine with a specific antibody but is not an **immunogen** (def. 2), i.e. it is not by itself able to stimulate antibody production though it may do so if combined with a **carrier** (def. 8). In this sense the term includes **hapten**. —**antigenic** *adj.*

antigen–antibody complex *or* **immune complex** any specific macromolecular complex of antigen and antibody. It may be soluble, especially in **antigen excess**, or insoluble (as a precipitate) when antigen and antibody are present in optimal proportions. Components of **complement** may bind to antigen–antibody complexes. *See also* **immune complex-mediated hypersensitivity**.

antigen-binding capacity *abbr.*: ABC; the total amount of antibody in a preparation, e.g. serum, based on a determination of the amount of antigen bound by unit amount of the preparation.

antigen excess the condition when a mixture of antigen and antibody contains sufficient antigen to combine with all the combining sites of the specific antibody molecules, leaving some free uncombined antigenic determinants and resulting in the formation of soluble antigen–antibody complexes. This is the explanation for the type of 'precipitin' curve when increasing amounts of antigen are incubated with a fixed amount of antibody and the amount of precipitate is measured.

antigenic determinant any specific chemical structure within, and generally small in relation to, an antigen molecule that is recognizable by a combining site of an antibody, or T-cell or B-cell receptor, and at which combination takes place. It determines the specificity of the antibody–antigen reaction. Several different antigenic determinants may be carried by a single molecule of antigen. *See also* **epitope**.

antigenic drift any of the minor changes in the antigenicity of influenza virus that result from spontaneous mutation, with corresponding minor changes in the amino-acid sequence of the viral hemagglutinin. *Compare* **antigenic shift**.

antigenicity the capacity of an agent to stimulate the formation of specific antibodies to itself.

antigenic shift any of the major changes in the antigenicity of influenza virus that result from spontaneous mutation, with corresponding major changes in the amino-acid sequence of the viral hemagglutinin. *Compare* **antigenic drift**.

(antigen-independent) mitogenic factor a **lymphokine** that acts as a **mitogen** for lymphocytes.

antigen-presenting cell *abbr.*: APC; a cell, especially a macrophage or dendritic cell, that recognizes an antigen to be targeted for neutralization. It takes up the antigen and processes it, incorporating antigen fragments into its own membrane and presenting them in association with class II **major histocompatibility complex** molecules to T lymphocytes, which are then stimulated to mount a response.

antigibberellin any of the organic compounds that cause plants to grow with thick stems or with an appearance differing from that obtained with **gibberellin**. The effect can usually be reversed by gibberellin.

antiglobulin consumption test a serological method for demonstrating antibody (globulin) attachment to cells. It is based on showing that antiglobulin is removed from solution on addition of the cells in question.

antiglobulin test *or* **Coombs test** a test for the presence of incomplete **antibody** against red blood cells. It entails the addition of heteroantibody to immunoglobulin (i.e. antiglobulin) to cause the agglutination of red blood cells previously coated with nonagglutinating incomplete antibody. *Compare* **double-antibody method**. [After Robin Royston Amos Coombs (b. 1921), British immunologist and hematologist who (with others) described it in 1945.]

antihemophilic factor *or* **antihemophilic factor A** *or* **antihemophilic globulin** *an alternative name for* factor VIII; *see* **blood clotting factors**.

antihemophilic factor B *an alternative name for* factor IX; *see* **blood coagulation**.

antihemophilic factor C *an alternative name for* factor XI; *see* **blood coagulation**.

antihemophilic globulin *an alternative name for* **antihemophilic factor**.

antihistamine any drug or other agent that antagonizes an action of histamine on the body. Antihistamines are used in the treatment of immediate-type hypersensitivity.

antihormone any substance that acts to attenuate hormone-induced responses, regardless of the mechanism involved.

anti-idiotype an antibody that reacts with **epitopes** on the V region of the **T-cell receptor**.

anti-inducer any compound that inhibits **operon** induction by competing for inducer binding to free repressor and stabilizing the repressor–operator complex.

antilipolytic **1** describing any agent that inhibits **lipolysis**. **2** an antilipolytic agent.

antilipotropic **1** describing any agent that is active metabolically in deflecting methyl groups from the synthesis of choline. **2** an antilipotropic agent.

antilogarithm *abbr.*: antilog; *symbol*: (decadic) lg^{-1}; (napierian) ln^{-1}; the number that is represented by a **logarithm**.

antilymphocyte globulin the globulin fraction of an **antilymphocyte serum**.

antilymphocyte serum *abbr.*: ALS; any serum containing antibodies to lymphocytes. It is used as a selective immunosuppressive agent.

anti-messenger DNA *abbr.*: amDNA; *an alternative name for* **complementary DNA**.

antimetabolite any substance that inhibits the utilization of a metabolite, e.g. by acting antagonistically through competition in a transport system or at a key enzyme site.

antimicrobial **1** describing a drug, antibiotic agent, physical process, radiation, etc. that is inimical to microbes. **2** any substance having antimicrobial properties.

antimicrobial spectrum a list of the types of microbes against which an antimicrobial agent is effective.

antimitotic **1** describing any agent that decreases the rate of mitosis. **2** an antimitotic agent.

antimonial **1** of, relating to, or containing antimony. **2** a drug containing antimony.

antimorph **1** a mutant gene producing an effect opposite to the wild-type gene at the same locus. *Compare* **allele**. **2** *obsolete term for* an **enantiomorph**.

antimutagen any agent (often a purine nucleoside) that can decrease the rate of induced or spontaneous mutation.

antimutator gene any mutant gene that decreases the mutation rate.

antimycin any member of a group of antibiotics produced by *Streptomyces* spp. They associate strongly with mitochondria and block the passage of electrons from cytochrome *b* to cytochrome c_1; as little as 7 pmol antimycin A_1 per gram of mitochondrial protein is effective. They are used experimentally to distinguish between events in the earlier and later parts of the electron-transport chain.

antineoplastic **1** describing any drug or other treatment that prevents or limits the growth of a neoplasm. **2** an antineoplastic agent.

antinuclear factor *or* **antinuclear antibody** any antibody that reacts with a component of the cell nucleus.

antioxidant *or* **antoxidant** any substance, often an organic compound, that opposes oxidation or inhibits reactions brought about by dioxygen or peroxides. Usually the antioxidant is effective because it can itself be more easily oxidized than the substance protected. The term is often applied to components that can trap **free radicals**, such as α-tocopherol (*see* **vitamin E**), thereby breaking the chain reaction that normally leads to extensive biological damage. The mechanism by which the free-radical scavenger is discharged of its free radical is not clear, but it is likely that ascorbate, glutathione, and,

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ultimately, NAD^+ and the **respiratory chain** are involved. Compounds such as di-*tert*-butyl-*p*-cresol act as antioxidants and are often added to protect labile compounds during storage or incubation. *See also* **quinhydrone**.

antiparallel **1** *(in biochemistry)* (describing of a pair of parallel linear structures, such as two polynucleotide or polypeptide chains, having directional polarity or asymmetry in opposite directions. **2** *(in quantum physics)* (of the spins of a pair of electrons occupying the same atomic or molecular orbital) described by different spin quantum numbers. *Compare* **parallel** (def. 2). —**antiparallelism** *n.*

antiperiplanar *see* **conformation**.

antipernicious anemia factor *former name for* **vitamin B_{12}**.

antiport *or* **countertransport** the process of coupled solute translocation in which two solutes equilibrate across an osmotic barrier, the translocation of one solute being coupled to the translocation of the other in the opposite direction. *Compare* **symport**.

antiporter any substance or structural feature, but usually a protein, that promotes the exchange diffusion of two specific substances across a membrane by **antiport**. The convention for denoting such a protein (e.g. a tetracycline-resistance protein) is tetracycline/H^+ antiporter.

antirachitic **1** describing any agent that opposes or prevents the development of **rickets**. **2** any agent with antirachitic properties.

antirachitic factor *or* **antirachitic vitamin** *former term for* any substance with **vitamin D** activity.

antirepressor any gene product that acts to decrease repression by a repressor of gene expression.

antirestriction the process whereby a host bacterium is prevented from inactivating foreign duplex DNA; i.e. the prevention of **restriction**. It is commonly achieved by **host-controlled modification** of the DNA, but in certain cases a specific bacteriophage-coded **antirestriction protein** is produced that directly inhibits the host's **restriction endonuclease**.

antirestriction protein *see* **antirestriction**.

anti-RNA single-stranded RNA complementary to mRNA. *See* **antisense RNA**.

antiscorbutic **1** describing an agent that opposes or prevents the development of **scurvy**. **2** any agent with antiscorbutic properties.

antiscorbutic factor *or* **antiscorbutic vitamin** *former term for* any substance with **vitamin C** activity.

antisense DNA *see* **noncoding strand**.

antisense oligonucleotide an oligoribonucleotide, or an analogue of one, having properties similar to those of **antisense RNA**.

antisense RNA *or* **messenger-RNA-interfering complementary RNA** (*abbr.*: micRNA) an artificial single-stranded RNA molecule complementary in sequence to all or part of a molecule of messenger RNA or of some other specific RNA transcript of a gene. It can therefore hybridize with the specific RNA and so interfere with the latter's actions or reactions. *Compare* **complementary RNA**.

antisense strand *see* **noncoding strand**.

antisepsis the elimination of pathogenic and other microorganisms using chemical or physical methods; the promotion of **asepsis**.

antiseptic **1** of, relating to, or bringing about **antisepsis**. **2** any chemical agent used in antisepsis, especially one that can be safely applied to the skin.

antiserum (*pl.* **antisera** *or* (*esp. US*) **antiserums**) serum that contains a high level of antibodies, usually antibodies against specific antigens.

antisigma factor a protein that interferes with the recognition of initiation sites by the **sigma factor** of DNA-dependent RNA polymerase.

antistasin *the generic name for* a family of potent inhibitors of factor Xa. Antistasins are isolated from leeches, and the name was first given to a 119-amino-acid protein present in salivary gland of the Mexican leech *Haementeria officinalis*; the protein has 20 cysteine residues, all in disulfide bridges (probably characteristic of the family). It appears to present a **bait**-like structure to factor Xa, which cleaves it at Arg^{34}. The 3-D structure has been partially solved, indicating a reactive site in domain I, sequence CRKTC. Antistasins have been considered as possible chemotherapeutic anticoagulants but have strong metastatic activity. Example, **ghilanten** from the Amazonian leech *H. ghillianii*: database code ANTA_HAEGH, 119 amino acids (13.30 kDa).

antistreptolysin-O *abbr.*: ASO; antibody formed against streptolysin-O. *See* **streptolysin**.

antisuppressor any mutation that diminishes the effects of a suppressor of gene expression.

antitemplate strand *see* **coding strand**.

antiterminator (*or* **antitermination factor**) a protein that prevents the termination of RNA synthesis. It is found as a regulatory device in, e.g., phage lambda, enabling a terminator to be masked from RNA polymerase so that distal genes can be expressed. Antiterminators are associated with switches from early to middle expression following induction (gene N product, database code REGN_LAMBD, 107 amino acids (12.24 kDa)) and from early to late expression (gene Q product, database code REGQ_LAMBD, 207 amino acids (22.45 kDa)). The N system is referred to under ***nus***. Antitermination is an important mechanism in the reproduction of some bacteriophages, allowing RNA polymerase to read through the terminator to the immediate early genes of the phage and thus initiate production of the mature phage with consequent cell lysis.

antithrombin III *or* **heparin cofactor** *or* **factor Xa inhibitor** a 62 kDa protein inhibitor of serine proteinases, normally present in plasma, that reacts with factor IIa (thrombin), and also factors IXa, Xa, XIa, and XIIa to form inert 1:1 stoichiometric complexes. The formation of complexes is slow in the absence of heparin but very fast in its presence. Example from *Bos taurus*: ANT3_BOVIN, 433 amino acids (49.13 kDa).

antitoxin any antibody to a **toxin** of a (micro)organism that neutralizes the toxin both *in vitro* and *in vivo*.

α_1-antitrypsin *or* **α_1-proteinase inhibitor** a major α_1-globulin, normally present in human plasma, that inhibits many serine proteinases, including trypsin but especially elastase, and is the archetypal **serpin**. Its concentration rises dramatically in response to infection or tissue injury (*compare* **acute-phase protein**). A 51 kDa glycoprotein, its prime physiological role is to inhibit elastase released by neutrophil leukocytes. In humans, its synthesis is controlled by an autosomal allelic system and over 20 different phenotypes have been classified, one of which is associated with emphysema of early onset; in particular, the so-called Z mutant (Glu → Lys at position 342) is associated with a decreased level of α-antitrypsin in the blood. Smoking tends to cause oxidation of Met^{358}, by increasing hydrogen peroxide formation by lung neutrophils, and this leads to a less active α_1-antitrypsin and hence reduced inhibition of elastase. Excessive activity of elastase may damage lung tissue, resulting in emphysema. Thus smoking is associated with emphysema of early onset. Individuals who are homozygous for the Z mutant and who also smoke suffer decreased levels of a less active anti-elastase and have a high probability of developing emphysema. The protein has two chains; examples (human): chain A, database code NRL_7APIA, 339 amino acids (38.09 kDa); 3-D structure known; chain B, database code NRL_7APIB, 36 amino acids (4.13 kDa); 3-D structure known.

antitussive **1** relieving or suppressing coughing. **2** an agent with antitussive properties.

antivitamin any agent that antagonizes a specific vitamin. Sometimes it is a structural analogue of the vitamin and a competitive inhibitor of the vitamin's action.

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antixerophthalmic factor *former term for* any substance with **vitamin A** activity.

antoxidant *a variant spelling of* **antioxidant**.

antrin a decapeptide, isolated from rat gastric antrum. It has the sequence

Ala-Pro-Ser-Asp-Pro-Arg-Leu-Arg-Gln-Phe

and is identical to residues 25–34 of preprosomatostatin (*see* ***somatostatin***).

anucleate *or* **anucleated** lacking a **nucleus**.

anucleolate lacking a **nucleolus**.

AOX *abbr. for* **alcohol oxidase**.

AP *see* **AP endonuclease**, **AP protein**.

6-APA *abbr. for* 6-aminopenicillanic acid.

apamin a neurotoxin comprising about 2% of the dry mass of the venom of the honey bee (*Apis mellifera*). It is a highly basic octadecapeptide amide, structure

CNCKAPETALCAKKCEEH–NH_2,

containing two disulfide bridges (between Cys residues 1 and 11, and 3 and 15), and is the smallest neurotoxic peptide known. *Compare* **melittin**.

APC *abbr. for* **1** activated protein C. **2** antigen-presenting cell.

APC the human gene for adenomatous polyposis coli protein. The gene is a tumour suppressor, and mutations are associated with familial adenomatous polyposis, Gardner's syndrome, etc. and contribute to colorectal cancer. The protein product is of unknown function and has serine phosphorylation, glycosylation, and myristoylation sites. It is concentrated in the basolateral region of crypt epithelial cells. Product database code: APC_HUMAN, 2843 amino acids (311.32 kDa).

Ape *symbol for* a residue of the α-amino acid L-α-aminovaleric acid, L-2-aminopentanoic acid.

AP endonuclease *abbr. for* apyrimidinic or apurinic nuclease; any of various DNA repair enzymes that make breaks at sites generated by DNA glycosylase. There are three types: (1) ***deoxyribonuclease V***; (2) exodeoxynuclease III (endonuclease activity) *see* **deoxyribonuclease** III; and (3) DNA-(apurinic or apyrimidinic site) lyase, EC 4.2.99.18; *other names*: AP lyase; AP endonuclease class I; endodeoxyribonuclease (apurinic or apyrimidinic); deoxyribonuclease (apurinic or apyrimidinic); *Escherichia coli* endonuclease III; phage-T4 UV endonuclease; *Micrococcus luteus* UV endonuclease. They catalyse a reaction in which the C–O–P bond 3′ to the apurinic or apyrimidinic site in DNA is broken by a β-elimination reaction, leaving a 3′-terminal unsaturated sugar and a product with a terminal 5′-phosphate. Example: endonuclease III from *E. coli*; this binds a Fe_4S_4 cluster, which is not important for the catalytic activity but which is probably involved in the proper positioning of the enzyme along the DNA: database code END3_ECOLI, 211 amino acids (23.53 kDa).

A peptide the octadecapeptide cleaved from the α chains of a fibrinogen molecule when it is converted into fibrin by the proteolytic action of thrombin. *Compare* **B peptide**.

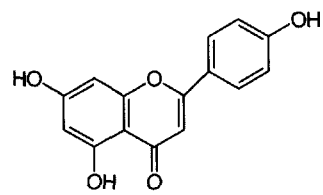
aperture *(in physics)* **1** an opening in an optical or other similar instrument that controls the amount of radiation entering or leaving it. **2** the diameter of the refracting surface of a lens or reflecting surface of a mirror. *See also* **f-number**.

aphidicolin a potent antiviral and antimitotic agent, first isolated as an antibiotic from the fungus *Cephalosporium aphidicola*. It inhibits eukaryotic DNA polymerase.

Api *symbol for* D-apiose.

apical surface the surface of an epithelial cell that faces the lumen.

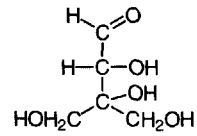
apigenin 4′,5,7-trihydroxyflavone; the aglycon of **apiin**. It inhibits cyclooxygenase and estrogen synthase. *See* **D-apiose**.



apigenin

apiin apigenin-7-apiosylglucoside, apioside; the name is derived from *Apium* (celery) from which apiin is isolated. *See also* **apigenin**, **apiose**.

apiose *symbol*: Api; the D isomer, 3-*C*-(hydroxymethyl)-D-*glycero*-aldotetrose is a branched carbon chain sugar that occurs widely in plants either in glycosides or polysaccharides. It is a component of **apiin**.



D-apiose

aplasia incomplete or deficient development of an organ or tissue.

aplastic **1** not showing normal growth or change in structure. **2** relating to or showing **aplasia**.

Apm *symbol for* a residue of the α-amino acid α-aminopimelic acid, 2-aminoheptanedioic acid.

A_2pm *or* **Dpm** *symbol for* the di(α-amino acid) α,ε-diaminopimelic acid, 2,6-diaminoheptanedioic acid.

APMSF *p*-amidinophenylmethylsulfonylfluoride; a specific irreversible inhibitor of trypsin-like serine endopeptidases, with greater inhibitory activity than **phenylmethylsulfonylfluoride**.

apo+ *prefix* denoting detached, separate. It is used especially of enzymes and other proteins. For example, apocarboxylase is the protein part of the holoenzyme carboxylase, i.e. it lacks the covalently bound biotin residue(s). Apoferritin is a 450 kDa protein with 24 identical subunits, that combines with ferric hydroxide-phosphate to form **ferritin**. *See also* **apoenzyme**.

Apo(a) *or* **lipoprotein(a)** a serine endopeptidase (EC 3.4.21.–) related to **plasminogen**, having 37 repeats of plasminogen **kringle** domains and capable of cleaving **fibrinogen**. It is covalently linked (by disulfide bond) to apolipoprotein B-100. Its plasma concentration is related to the incidence of atherosclerosis. Example from human: database code APOA_HUMAN, 4577 amino acids (500.77 kDa).

apocrine **1** describing a type of secretion that entails loss of part of the cytoplasm of the secretory cell. **2** describing a gland made up of such cells. *Compare* **eccrine**, **holocrine**, **merocrine**.

apoenzyme the protein part of an enzyme that forms a catalytically active enzyme (holoenzyme) when combined with an activator, a coenzyme, or a prosthetic group. It determines the specificity of the catalytic system.

apoferritin *see* **ferritin**.

apolar **1** lacking poles, especially of nerve cells. **2** **nonpolar**.

apolar interaction any of the entropy-driven interactions between nonpolar parts of molecules when in polar solvents. It is important in maintaining the structure of protein molecules in polar solvents, in antigen–antibody interactions, in virus–protein and enzyme–subunit aggregation and disaggregation, and in determining enzyme specificity.

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apolipophorin a protein component of **lipophorin**. This protein increases the lipid-carrying capacity of lipophorin by covering the expanding hydrophobic surface resulting from diacylglycerol uptake. Example (precursor) apolipophorin IIIB from *Locusta migratoria*: database code APL3_LOCMI, 179 amino acids (19.09 kDa).

apolipoprotein the protein component of any lipoprotein, but especially of plasma lipoproteins. The latter are designated by the abbreviation 'Apo', e.g. ApoA (for apolipoprotein A), ApoB, etc., and are subdivided into subtypes, e.g. ApoA-I for apolipoprotein A, subtype I. See following entries for individual types of apolipoprotein.

apolipoprotein A-I *abbr.*: ApoA-I; the major protein of plasma **high-density lipoprotein** (HDL), also found in chylomicrons. It is synthesized in the liver and small intestine, and participates in the reverse transport of cholesterol from tissues to the liver by promoting cholesterol efflux from tissues; it acts as a cofactor for **lecithin–cholesterol acyltransferase**. Deficiency of ApoA-I is associated with **Tangier disease**. Example (precursor) from human: database code APA1_HUMAN, 267 amino acids (30.74 kDa).

apolipoprotein A-II *abbr.*: ApoA-II; an apolipoprotein associated with **high-density lipoprotein**, which it stabilizes. It is a homodimer (disulfide linked). Example from human: database code APA2_HUMAN, 100 amino acids (11.62 kDa).

apolipoprotein A-IV *abbr.*: ApoA-IV; an apolipoprotein that is a major component of **high-density lipoprotein** and chylomicrons. It is involved in the catabolism of chylomicrons and very-low-density lipoprotein, being required for efficient activation of **lipoprotein lipase** by apolipoprotein C-II. It is a potent activator of **lecithin–cholesterol acyltransferase**. Example from human: database code APA4_HUMAN, 396 amino acids (45.32 kDa).

apolipoprotein B *abbr.*: ApoB; a major protein constituent of chylomicrons, very-low-density lipoprotein, and low-density lipoprotein. It exists in two forms, B-100 (amino acids 28–4563 of the sequence) and B-48 (amino acids 28–2179); the latter is of intestinal origin and derived from editing of mRNA to form an internal stop codon. Excessive plasma levels occur in familial **hypercholesterolemia**. Example from human: database code APB_HUMAN, 4563 amino acids (514.97 kDa).

apolipoprotein C-I *abbr.*: ApoC-I; a component of chylomicrons and very-low-density lipoprotein (VLDL), synthesized mainly in liver. It modulates the interaction of apolipoprotein E with β-migrating VLDL and inhibits binding of β-VLDL to low-density lipoprotein receptor-related protein. Example from human: database code APC1_HUMAN, 83 amino acids (9.32 kDa).

apolipoprotein C-II *abbr.*: ApoC-II; a component of very-low-density lipoprotein (VLDL) and an activator of several triacylglycerol lipases. It has a reversible association with plasma chylomicrons, VLDL, and high-density lipoprotein. Deficiency results in hypertriglyceridemia, xanthomas, and increased risk of pancreatitis and early atherosclerosis (hyperlipoproteinemia, type IB). Example from human: database code APC2_HUMAN, 101 amino acids (11.27 kDa).

apolipoprotein C-III *abbr.*: ApoC-III; an apolipoprotein that constitutes 50% of the protein fraction of very-low-density lipoprotein. It binds to sugar and sialic-acid residues and inhibits lipoprotein and hepatic lipases. Example from human: database code APC3_HUMAN, 99 amino acids (10.84 kDa).

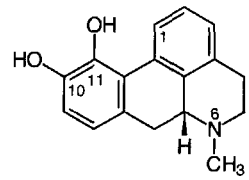
apolipoprotein D *abbr.*: ApoD; an apolipoprotein that occurs in a macromolecular complex with **lecithin–cholesterol acyltransferase** and in high-density lipoprotein. It is a **lipocalin** of known 3-D structure, probably involved in the transport and binding of bilin. The homodimer shows wide tissue distribution. Example from human: database code APD_HUMAN, 189 amino acids (21.25 kDa).

apolipoprotein E *abbr.*: ApoE; an apolipoprotein that constitutes 10–20% of very-low-density lipoprotein. It mediates binding, internalization, and catabolism of lipoprotein particles and is a ligand for the low-density lipoprotein (ApoB/E) receptor and for the ApoE receptor (chylomicron remnant) of hepatic tissues. It is present in brain and may have a role in cholesterol transport. *O*-Glycoside and sialic-acid residues occur, but it is de-sialylated in plasma. It has nine allelic variants and two of these are associated with hyperlipoproteinemia type III. The 3-D structure is known; it contains a heparin-binding motif. Example from human: database code APE_HUMAN, 317 amino acids (36.11 kDa).

apolipoprotein H *abbr.*: ApoH; *other names*: β_2-glycoprotein II precursor; APC inhibitor (*see* **activated protein C**). An apolipoprotein that binds to anions such as heparin and phospholipids. It may prevent activation of the intrinsic blood coagulation cascade by binding to phospholipids on the surface of damaged cells. *See also* **amyloid A protein**.

apolipoprotein receptor *see* **LDL receptor**, **VLDL receptor**.

apomorphine 6a*β*-aporphine-10,11-diol; 5,6,6a,7-tetrahydro-6-methyl-4*H*-dibenzo[*de*,*g*]quinoline-10,11-diol; a synthetic opiate. The (*R*)-enantiomer is a potent dopamine receptor agonist, noted for its powerful emetic effects.



apoplast the nonliving part of plant tissue, external to the plasmalemma and composed of the cell walls, the intercellular spaces, and the lumen of dead structures such as xylem cells.

apoprotein the protein part of a **conjugated protein**.

apoptosis cell death may occur by accident, by cell **necrosis**, or by an intracellular controlled process characterized by a condensation and subsequent fragmentation of the cell nucleus during which the plasma membrane remains intact. The term apoptosis may be used broadly to encompass all forms of such normal or pathological cell death or may be confined to those processes involving morphological changes such as occur in normal animal development. A cascade of **caspases**, (**cysteine endopeptidases** that cleave at specific aspartic residues hence the name) is involved. In this cascade, caspases cleave procaspases to form additional caspases. Some of the caspases thus formed cleave other proteins, including deoxyribonucleases. [From **apo-** + Greek *ptosis*, falling.]

aporepressor the protein component of a complex that can act to inhibit gene expression. *See also* **repressor**.

apparent describing a physical quantity, especially an association constant, dissociation constant, equilibrium constant, etc., that has been determined under particular experimental conditions and hence is not the true (i.e. thermodynamic) constant. *See* **equilibrium constant**.

apparent exchangeable mass a term used in tracer kinetics in whole animals for a mass obtained by dividing the quantity of administered radioactivity that is retained by the specific activity of the tracer in the (blood) plasma. It equals the total exchangeable mass when the specific activities are equal throughout the system. *Compare* **compartment**.

apparent molecular weight *former name for* **apparent relative molecular mass**.

apparent relative molecular mass **relative molecular mass** that has been determined by a method that does not make allowance for any nonideality of the system.

apple domains sequences of 90 or 91 amino-acid residues that contain three highly conserved disulfide bonds linking the first and sixth, second and fifth, and third and fourth cysteine

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residues present in each repeat. They can be drawn in the shape of an apple. Four are present in human kallikrein and in human coagulation factor XI. *See also* **Appendix E**.

applicator any device or instrument, such as a comb, rod, spatula, or tube, for applying samples in a reproducible manner to a small defined area, e.g. in chromatography, or for applying something to a particular part of the body.

approach to (sedimentation) equilibrium method *or* **Archibald method** a method for determining the relative molecular masses of (macro)molecules by sedimentation in an ultracentrifuge, by measuring the depletion of the macromolecules from the meniscus and their accumulation at the cell bottom. Its advantage is that only very short periods of sedimentation are required. [After William James Archibald (1912–)]

AP protein *abbr. for* activator protein, one of two **transcription factors**; AP1, a product of c-*jun* (*see* ***JUN***), interacts with Fos (product of c-*fos*) to form a dimer. It harbours two functional domains, one responsible for DNA binding and one for binding to Fos, and includes a leucine zipper. Example from human: database code TAP1_HUMAN, 331 amino acids (35.63 kDa). AP2 interacts with inducible viral and cellular enhancer elements to stimulate transcription of selected genes. It contains the consensus binding sequence CCCAGGC and a helix-span-helix motif. Example from human: database code TAP2_HUMAN, 437 amino acids (48.01 kDa).

A_2pr *or* **Dpr** *symbol for* a residue of the α,β-diamino acid L-α,β-diaminopropionic acid; L-2,3-diaminopropanoic acid.

aprotic describing a substance, especially a solvent, that is unable to act as a proton acceptor or donor.

aprotinin a proteinase inhibitor derived from animal tissues. It is a basic polypeptide of known sequence of 58 amino-acid residues (≈6.5 kDa) that exists as a dimeric aggregate. It is stable in acid or neutral media and at high temperature, and it inhibits kallikrein, trypsin, chymotrypsin, plasmin, and, to a lesser extent, papain. *See also* **Trasylol**.

APRT *abbr. for* adenine phosphoribosyltransferase.

APS *abbr. for* adenosine 5′-phosphosulfate.

APT *abbr. for* alum-precipitated toxoid.

aptitude *(in microbiology)* the specific physiological state of a **lysogenic bacterium** that enables it, upon induction, to react so as to produce infectious bacteriophage particles.

apud *or* **APUD** *abbr. for* amine precursor uptake and decarboxylation; designating any of a series of cells that produce peptides and/or amines active as hormones or neurotransmitters, share a spectrum of cytochemical qualities, and appear in many cases to have a common embryological origin. They are thought to include the A, B, and D cells of the endocrine pancreas, the C cells of the thyroid, and the various hormone-producing cells of the pituitary and the gut.

apudoma *any tumour of an* ***apud*** *cell, e.g. a gastrinoma, glucagonoma, insulinoma, or VIPoma.*

apurinic acid a DNA derivative in which all the purine bases have been removed by selective hydrolysis, leaving the pyrimidine–deoxyribose bonds and the phosphodiester bonds of the backbone intact. It results from the gentle acid hydrolysis of DNA at pH 3.0.

apurinic endonuclease *see* **AP endonuclease**.

apyrase EC 3.6.1.5; *other names*: ATP-diphosphatase; adenosine diphosphatase (*abbr.*: ADPase); a Ca^{2+}-requiring enzyme that catalyses the hydrolysis of ATP to AMP and 2 orthophosphate. It also hydrolyses other nucleotides, especially ADP to AMP and orthophosphate. It was originally identified in plants, especially potatoes, but enzymes of this type have also been found in animals, e.g. as a surface enzyme on lymphoid cells identical to CD39, and as a secreted enzyme of the yellow-fever mosquito, *Aedes aegypti*. It is used in platelet incubations to destroy ADP. Example from *A. aegypti*: database code APY_AEDAE, 562 amino acids (62.73 kDa).

apyrimidinic acid a DNA derivative from which the pyrimidine bases have been removed chemically, leaving the purine–deoxyribose bonds and the phosphodiester bonds of the backbone intact.

apyrimidinic endonuclease *see* **AP endonuclease**.

aq *(in chemistry) abbr. for* aqueous.

aqua+ *comb. form* **1** denoting acting on or reacting with water. **2** denoting presence of water as a neutral ligand in a coordination entity, e.g. aquacobalamin. The number of water molecules per entity is indicated by an approximate multiplying prefix, e.g. hexaquachromium trichloride.

aquacide a substance that when added to a mixture removes water molecules, usually by forming a compound with the elements of water. —**aquacidal** *adj.*

aquaporin any of a class of **CHIPS** that are specific for the transfer of water. Example, specific for erythrocytes and kidney proximal tubule, from human: database code AQP1_HUMAN, 269 amino acids (28.49 kDa).

aqueous **1** of, having the characteristics of, or relating to water. **2** dissolved in or mixed with water. **3** *or* **aqueous humour** the fluid occupying the space between the crystalline lens and the cornea of the eye.

aquo+ *comb. form* **1** containing one or more water molecules in a coordination complex. **2** *(in chemical nomenclature)* derived from water.

aquo-ion a complex ion containing one or more water molecules held by coordination.

Ar *symbol for* **1** argon. **2** aryl.

Ara *symbol for* arabinose.

ara a plant gene related to ***ras***.

araBAD an operon characterized in *Escherichia coli* and encoding L-ribulokinase, L-arabinose isomerase, and L-ribulose 5-phosphate 4-epimerase, three of the enzymes that metabolize arabinose. *See also* ***araC***.

Arabidopsis thaliana a small Cruciferous plant (common wall cress) widely used in plant genetic research because of its small genome and very short generation time.

arabin+ *a variant (before a vowel) of* **arabino+**.

arabinan a branched homopolymer of L-arabinose found in plant pectins.

arabinaric acid *see* **aldaric acid**.

arabino+ *or (before a vowel)* **arabin+** *comb. form* indicating arabinose.

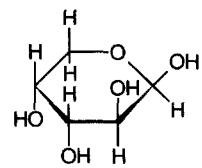
arabino- *prefix (in chemical nomenclature)* indicating a chemical compound containing a particular configuration of a set of three (usually) contiguous >CHOH groups, as in the acyclic form of D- or L-arabinose. *See* **monosaccharide**.

arabinofuranosylcytosine cytosine arabinoside; *see* **cytarabine**.

arabinogalactan any member of a subgroup of plant hemicelluloses that contain arabinose and galactose and are particularly abundant in larch.

arabinonucleoside the 1-β-D-arabino-*N*-furanoside of a purine or pyrimidine base. It is a structural analogue of a **riboside**.

arabinose *arabino*-pentose; a monosaccharide. L-Arabinose occurs free, e.g. in the heartwood of many conifers, and in the combined state, in both furanose and pyranose forms, as a constituent of various plant hemicelluloses, bacterial polysaccharides, etc. D-Arabinose occurs to some extent in plant glycosides and is a constituent of the **arabinonucleosides**.



β-D-arabinose

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D-arabinose isomerase EC 5.3.1.3; *systematic name*: D-arabinose ketol-isomerase. An enzyme that catalyses the reaction:

D-arabinose = D-ribulose.

See also **L-arabinose isomerase**.

L-arabinose isomerase EC 5.3.1.4; *systematic name*: L-arabinose ketol-isomerase. An enzyme that catalyses the reaction:

L-arabinose = L-ribulose.

It initiates the metabolism of L-arabinose. Example from *Escherichia coli*: database code ARAA_ECOLI, 500 amino acids (55.98 kDa). *See also* ***araBAD***, **D-arabinose isomerase**.

arabinose-5-phosphate isomerase EC 5.3.1.13; *systematic name*: D-arabinose-5-phosphate ketol-isomerase. An enzyme that catalyses the reaction:

D-arabinose 5-phosphate = D-ribulose 5-phosphate.

arabinoside any glycoside derived from arabinose.

arabinoxylan any of various neutral polysaccharides that occur in association with acidic polysaccharides in cereal gums. They consist of a chain of (1→4)-linked β-D-xylan units with single α-L-arabinofuranosyl groups in (1→3) linkage.

arabitol *or* **arabinitol** *arabino*-pentitol; the pentitol formally derived by reduction of the aldehyde group of arabinose or lyxose. The D enantiomer is present in lichens and mushrooms.

araC the gene for the AraC protein, which acts as a regulator of expression of the *araBAD* operon and of *araC* itself. AraC acts as both a repressor (when intracellular arabinose levels are low), binding to *araO* operator sites, and an activator (in the presence of arabinose), when bound to the *araI* site, but only in the presence of cyclic AMP–CRP complex. It is a typical **helix-turn-helix** DNA-binding regulatory protein. Database code ARAC_ECOLI, 292 amino acids (33.35 kDa).

ara-C *abbr. for* arabinosylfuranosylcytosine.

arachain an unclassified proteinase obtained from the peanut, *Arachis hypogaea*.

arachidic acid *the trivial name for* eicosanoic acid; CH_3–$[CH_2]_{18}$–COOH; a constituent of arachis oil (from the peanut, *Arachis hypogaea*) and other oils. *See also* **arachidoyl**.

arachidonate 5-lipoxygenase EC 1.13.11.34; *other names*: 5-lipoxygenase; leukotriene-A_4 synthase; a **lipoxygenase** (def. 2) enzyme that catalyses the reaction of arachidonate with dioxygen to form (6*E*,8*Z*,11*Z*,14*Z*)-(5*S*)-5-hydroperoxyeicosa-6,8,11,14-tetraenoate. Iron is a cofactor. Example from human: database code LOX5_HUMAN, 673 amino acids (77.76 kDa).

arachidonate 12-lipoxygenase EC 1.13.11.31; *other name*: 12-lipoxygenase; a **lipoxygenase** (def. 2) enzyme that catalyses the reaction of arachidonate with dioxygen to form (5*Z*,8*Z*,10*E*,14*Z*)-(12*S*)-12-hydroperoxyeicosa-5,8,10,14-tetraenoate. Iron is a cofactor. Example from human: database code LOX2_HUMAN, 662 amino acids (75.45 kDa).

arachidonate 15-lipoxygenase EC 1.13.11.33; *other names*: arachidonate ω-6 lipoxygenase; 6-lipoxygenase; a **lipoxygenase** (def. 2) enzyme that catalyses the reaction of arachidonate with dioxygen to form (5*Z*,8*Z*,11*Z*,13*E*)-(15*S*)-15-hydroperoxyeicosa-5,8,11,13-tetraenoate. Iron is a cofactor. Example from human: database code LOX1_ HUMAN, 661 amino acids (74.59 kDa).

arachidonic acid *see* **eicosatetraenoic acid**.

arachidonoyl *symbol*: Δ_4Ach; *the trivial name for* (*all-Z*)-eicosa-5,8,11,14-tetraenoyl; CH_3–$[CH_2]_3$–$[CH_2$–CH=CH$]_4$–$[CH_2]_3$–CO– (*all-Z* isomer); the acyl group derived from arachidonic (i.e.(*all-Z*)-eicosa-5,8,11,14-tetraenoic) acid, a polyunsaturated, unbranched, acyclic, aliphatic acid. It occurs naturally in membrane phospholipids, and is a biochemical precursor of **prostaglandins** and **leukotrienes**. It is also present in mosses, algae, and ferns, but not in higher plants. Distinguish from **arachidonyl** and **arachidoyl**.

arachidonyl *the trivial name for* the alkyl group, CH_3–$[CH_2]_3$–$[CH_2$–CH=CH$]_4$–$[CH_2]_3$–CH_2–, derived from the alkenol analogue of arachidonic acid. Distinguish from **arachidonoyl**.

arachidoyl *or (formerly)* **arachidyl** *or* **arachyl** *symbol*: Ach; *the trivial name for* eicosanoyl; CH_3–$[CH_2]_{18}$–CO–; the acyl group derived from arachidic (*or* eicosanoic *or (formerly)* arachic) acid, a saturated, unbranched, acyclic, aliphatic acid. It occurs naturally as triarachin in certain seeds, oils, and butter fat. Arachidyl is now the name for the alkyl group, CH_3–$[CH_2]_{18}$–CH_2–. Distinguish from **arachidonyl**.

arachidyl *the trivial name for* the alkyl group, CH_3–$[CH_2]_{18}$–CH_2–, the alkanol analogue of arachidic acid. *See also* **arachidoyl**.

arachin the major protein of the groundnut, *Arachis hypogaea*, comprising a 345 kDa globulin with 12 subunits. Not all groundnuts contain the same arachin; there exist at least two forms, designated A and B, having similar amino-acid compositions and general properties but differing in their subunit composition. Examples of subunits: database code ARA1_ ARAHY, 176 amino acids (20.86 kDa); ARA5_ARAHY, 201 amino acids (22.22 kDa). *See also* **conarachin**.

Arber, Werner (1929–), Swiss microbiologist; Nobel Laureate in Physiology or Medicine (1978) jointly with D. Nathans and H. O. Smith 'for the discovery of restriction enzymes and their application to problems of molecular genetics'.

arbovirus *abbr. for* arthropod-borne virus (a term formerly used for **togavirus**).

arc a continuous curved line, as part of a circle or ellipse; e.g. the line of antigen–antibody precipitate obtained in **immunodiffusion** or **immunoelectrophoresis**.

Archaea one of three primary kingdoms of cells, together with **Eukarya** and **Bacteria** (formerly **Eubacteria**), defined when cells are classified on the basis of rRNA sequence homologies. Archaea include all methanogens, extreme halophiles and most extreme thermophiles. Representative genera are: *Halobacterium*, *Methanobacterium*, *Sulfolobus*, *Thermoplasma*, and *Purodictium* (growth optimum = 105 °C); about 40 others are known. —**archaeal** *adj.*

Archaebacteria *former name for* **Archaea**.

Archibald method *see* **approach to (sedimentation) equilibrium method**.

Archimedes' principle the principle that when a body is partly or wholly immersed in a fluid there is an apparent loss of weight equal to the weight of the fluid displaced. [After Archimedes of Syracuse (?287–212 BC), Greek philosopher and applied mathematician.]

architectural gene a gene that determines the site of an enzyme within a cell.

A-region the presumptive initial oxidation site of a carcinogenic polycyclic aromatic hydrocarbon, on the terminal ring of the **bay region**, in the metabolic pathway leading to carcinogenesis (corresponding to what has sometimes been called the M-region). *Compare* **B-region**, **K-region**, **L-region**.

arenavirus any of a group of RNA viruses consisting of enveloped pleomorphic particles of 80–120 nm with helical nucleocapsids. The group includes Lassa virus and other viruses that spread to humans from rodents.

arene any monocyclic or polycyclic aromatic hydrocarbon.

arene oxide any epoxide formed by the addition of an atom of oxygen across any double bond of an **arene**.

ARF *abbr. for* ADP-ribosylation factor; a small monomeric cytosolic **GTPase** that, when bound to GTP, binds to the membranes of cells. It was originally discovered as a factor required for cholera toxin to ribosylate G_s, hence its name. Its structure is known and is highly conserved. It is a member of the ***RAS*** superfamily. Functions of ARF include regulation of membrane traffic in both endocytic and exocytic pathways, maintenance of organelle integrity, assembly of coat proteins (*see* **coatomer**), and activation of phospholipase D. *See* **phospholipase**.

Arg *symbol for* a residue of the α-amino acid L-arginine (alternative to R).

argentaffin cell a type of cell of the **apud** class, characterized by taking up silver stains with high affinity, without the addi-

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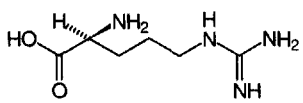
tion of reducing agent. [Named from Latin *argentum*, silver, and affinity.]

argentation chromatography any method of chromatography in which an adsorbent impregnated with silver nitrate is used to separate lipid classes according to the degree and geometry of their saturation. The technique may be used with either thin-layer chromatography or column chromatography, or in conjunction with gas–liquid chromatography.

arginase *abbr. (in clinical biochemistry)*: ARS; *recommended name for* EC 3.5.3.1; *other names*: arginine amidinase; *systematic name*: L-arginine amidinohydrolase. An enzyme that catalyses the hydrolysis of L-arginine to L-ornithine and urea; it also acts on α-*N*-substituted L-arginines and canavanine. It is a key enzyme in the **ornithine–urea cycle**, occurring in high concentrations in the liver of ureotelic vertebrates and being absent or nearly so from the liver of uricotelic species. It has a very wide species distribution. In humans it is defective in the inherited disorder argininemia. Examples: from *Bacillus subtilis*, database code ARGI_BACSU, 296 amino acids (32.15 kDa); from *Rattus norvegicus*, database code ARGI_RAT, 323 amino acids (34.97 kDa).

argininate **1** arginine anion; H_2N–C(=NH)–NH–$[CH_2]_3$–$CH(NH_2)$–COO^-. **2** any salt containing the arginine anion. **3** any ester of arginine.

arginine *trivial name for* N^5-amidino-ornithine; α-amino-δ-guanidinovaleric acid; 2-amino-5-guanidinopentanoic acid; H_2N–C(=NH)–NH–$[CH_2]_3$–$CH(NH_2)$–COOH; a chiral α-amino acid. L-Arginine *(symbol*: R *or* Arg), (*S*)-2-amino-5-guanidinopentanoic acid, is a coded amino acid found in peptide linkage in proteins; codon: AGA (not in mitochondria of fruit fly or mammals) or AGG (not in mitochondria of mammals); CGA, CGC, CGG, or CGU. It is an essential dietary amino acid in rats and probably in young humans, and is glucogenic in mammals. D-Arginine (*symbol*: D-Arg *or* DArg), (*R*)-2-amino-5-guanidinopentanoic acid, is not known to occur naturally.



L-arginine

arginine (base) the ionic form of an arginine residue when the guanidino group is unprotonated.

arginine carboxypeptidase *see* **lysine(arginine) carboxypeptidase**.

arginine kinase EC 2.7.3.3; an enzyme that catalyses a reaction between ATP and L-arginine to form ADP and N^{ω}-phospho-L-arginine. The latter compound may play a role in invertebrate muscle analogous to that of **creatine phosphate** in vertebrate muscle. Example from *Homarus gammarus* (European lobster): database code KARG_HOMGA, 355 amino acids (39.81 kDa).

arginine phosphate *former name (not recommended) for* **phosphoarginine**.

arginine–urea cycle *see* **ornithine–urea cycle**.

[8-arginine]vasopressin *or (less correctly)* **arginine vasopressin** *abbr.*: AVP *or* [Arg^8]vasopressin; the molecular form of **vasopressin** in which the variable eighth position in its amino-acid sequence is occupied by an arginine residue. This is the form present in humans and most other mammals.

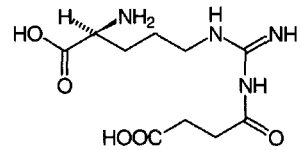
arginine vasotocin *or* ***[Arg^3]oxytocin*** *a pituitary peptide found in nonmammalian vertebrates with activity resembling both oxytocin and vasopressin.*

argininium **1** argininium(1+); the monocation of arginine. In theory, the term denotes any ion or mixture of ions formed from arginine and having a net charge of plus one, although in practice the predominant species is generally H_2N–C(=NH_2^+)–NH–$[CH_2]_3$–$CH(NH_3^+)$–COO^-. **2** *the systematic name for* argininium(2+); the dication of arginine.

arginino **1** N^2-arginino; the alkylamino group, H_2N–C(=NH)–NH–$[CH_2]_3$–CH(COOH)–NH–, derived from arginine by loss of a hydrogen atom from its α-amino group. **2** N^{ω}-arginino; the alkylguanidino group, HOOC–$CH(NH_2)$–$[CH_2]_3$–NH–C(=NH)–NH–, derived from arginine by loss of a hydrogen atom from its ω-amino group.

argininosuccinase EC 4.3.2.1; *systematic name*: *N*-(L-argininosuccinate) arginine lyase; *recommended name*: argininosuccinate lyase. An enzyme of the **ornithine–urea cycle** that catalyses the hydrolysis of *N*-(L-arginino)succinate to fumarate and L-arginine. Example (human) homotetramer (deficiency in argininosuccinicaciduria; very strong similarity to bird and reptile δ-crystallin): database code ARLY_HUMAN, 464 amino acids (51.78 kDa).

argininosuccinate 2-(N^{ω}-arginino)succinate; L-argininosuccinate is an intermediate in the **ornithine–urea cycle**, where it is synthesized by the enzymic condensation of L-citrulline with L-aspartate. *See* **arginosuccinate synthase**.



argininosuccinate synthase EC 6.3.4.5; *systematic name*: L-citrulline:L-aspartate ligase (AMP-forming); *other names*: argininosuccinate synthetase; citrulline–aspartate ligase. An enzyme of the **ornithine–urea cycle** that catalyses a reaction between ATP, L-citrulline, and L-aspartate to form L-argininosuccinate with release of AMP and pyrophosphate. A deficiency occurs in citrullinemia. Example (human) homotetramer: database code ASSY_HUMAN, 412 amino acids (46.37 kDa).

arginyl the acyl group, H_2N–C(=NH)–NH–$[CH_2]_3$–$CH(NH_2)$–CO–, derived from arginine.

argon detector *a sensitive detector used in gas chromatography that depends on the unique ionization properties of argon whereby its long-lived metastable excited atoms can transfer their energy of excitation by collision to other gas molecules of lower excitation potential. Thus argon can be used as the chromatographic carrier gas, the detector being an ionization chamber containing a source of ionizing radiation. Detectable changes of the level of ionization occur when the argon issuing from the column has another gas mixed with it. The detector was invented by James E. Lovelock. Its great advantage is that it does not depend on the chemical nature of the substances being separated.*

[Arg^8]vasopressin *abbr. for* [8-arginine]vasopressin.

arithmetic mean *see* ***mean***.

arm a base-paired segment of the clover-leaf model of transfer RNA. There are several such arms: **amino-acid arm**, **anticodon arm**, **dihydrouridine arm**, **extra arm**, and **TψC arm**.

ARNT *abbr. for* aryl-hydrocarbon receptor nuclear translocator; *other name*: dioxin receptor; a protein that mediates translocation of the **Ah receptor** from the cytoplasm to the nucleus after ligand has been bound. Example from human: ARNT_HUMAN, 789 amino acids (86.64 kDa).

A-RNA *abbr. for* A form of RNA.

aro1 *a fungal gene for aromatic amino-acid biosynthesis. It encodes a multifunctional protein for, e.g.,* **3-dehydroquinate synthase**, 3-dehydroquinase, **shikimate 5-dehydrogenase**, **shikimate kinase**, **EPSP synthase**. Example from *Emericella* (*Aspergillus*) *nidulans*: database code ARO1_EMENI, 1603 amino acids (174.89 kDa).

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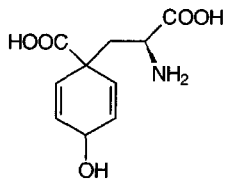
aroA–H, aroL *Escherichia coli* genes for **chorismate** synthesis.

arogenate *or* **pretyrosine** 3-(1′-carboxylato-4′-hydroxy-2′,5′-cyclohexadienyl)alanine; an intermediate in phenylalanine and tyrosine biosynthesis in *Euglena gracilis* and some other microorganisms, and in plants. It is formed by transamination of **prephenate** and is subsequently decarboxylated and converted to tyrosine, or converted to phenylalanine by dehydration and decarboxylation.



aromatic describing any organic compound characterized by one or more planar rings, each of which contains (usually) three conjugated double bonds and $(4n + 2)$ delocalized pi-electrons, where n is a small integer. They undergo substitution reactions more readily than addition reactions. The simplest member of the class is benzene. The term was originally used to distinguish fragrant compounds from **aliphatic** compounds. —**aromaticity** *n*.

aromatic amino acid any amino acid containing an aromatic ring. In proteins these are phenylalanine, tryptophan, and tyrosine.

aromatic-L-amino acid decarboxylase EC 4.1.1.28; *systematic name*: aromatic-L-amino-acid carboxy-lyase; *other names*: dopa decarboxylase; tryptophan decarboxylase; hydroxytryptophan decarboxylase. An enzyme that catalyses the decarboxylation of L-tryptophan to tryptamine; pyridoxal 5′-phosphate is a coenzyme. The popular name derives from the fact that the enzyme also acts on 5-hydroxy-L-tryptophan to yield 5-hydroxytryptamine and on dihydroxy-L-phenylalanine (dopa) to yield **dopamine**. Example from human: database code DCD_HUMAN, 480 amino acids (53.83 kDa); it is a homodimer, and structurally similar to certain other eukaryotic decarboxylases.

ARP_a *abbr. for* assimilatory regulatory protein a, i.e. ferredoxin-thioredoxin reductase.

ARP_b *abbr. for* assimilatory regulatory protein b, i.e. **thioredoxin**.

arrestin *or* **S antigen** any protein of a family that includes the Ca^{2+}-binding protein of rod-cell outer segments. It binds to photoactivated-phosphorylated rhodopsin, thereby apparently preventing the transducin-mediated activation of phosphodiesterase. It has been implicated in autoimmune uveitis. Example from human: database code ARRS_HUMAN, 405 amino acids (45.00 kDa). β-Arrestins are similar in their C-terminal parts to α-transducin and other purine-nucleotide-binding proteins. β-Arrestins regulate β-adrenergic receptor function; they seem to bind phosphorylated β-adrenergic receptors, thereby significantly impairing their capacity to activate G_S proteins. Example (β-arrestin 2) from human: database code ARRC_HUMAN, 409 amino acids (45.99 kDa).

Arrhenius, Svante August (1859–1927), Swedish chemist and physicist; Nobel Laureate in Chemistry (1903) 'in recognition of the extraordinary services he has rendered to the advancement of chemistry by his electrolytic theory of dissociation'.

(Arrhenius) activation energy *symbol:* E_a or E_A; *see* **Arrhenius equation**.

Arrhenius equation an equation representing the effect of temperature on the velocity of a chemical reaction. It may be expressed in the forms:

$$\mathrm{d}\ \ln k/\mathrm{d}T = E_a/RT^2 \qquad (1)$$

or

$$\mathrm{d}\ \ln k/\mathrm{d}(1/T) = -E_a/R \qquad (2)$$

or

$$k = Ae^{-E_a/RT} \qquad (3)$$

where k is the rate constant for the reaction, E_a is its **(Arrhenius) activation energy**, R is the gas constant, T is the thermodynamic temperature, and A is a constant termed the frequency factor or the pre-exponential factor. Version 2 may be integrated to:

$$\ln k = \ln A - E_a/RT \qquad (4).$$

Version 4 of the equation requires a plot of $\ln k$ against $1/T$, known as an **Arrhenius plot**, to be a straight line of slope $-E_a/R$, a relationship that has been shown to obtain for a considerable number of chemical reactions. *See also* **temperature coefficient of reaction**.

Arrhenius plot *see* **Arrhenius equation**.

ARS *abbr. for* **1** autonomously replicating sequence; any DNA sequence that can confer upon a plasmid the property of becoming a **replicon** in a particular host. The term is largely confined to fungal genetics. **2** *(in clinical biochemistry) abbr. for* arginase.

Arsenazo III 2,2′-(1,8-dihydroxy-3,6-disulfonaphthalene-2,7-bisazo)bisbenzenearsonic acid; an indicator substance used in the determination of low (micromolar) concentrations of free calcium ions. The free acid is purple; the calcium adduct is blue-violet.

arsenic *symbol*: As; a semi-metal element of group 15 of the IUPAC **periodic table**; atomic number 33; relative atomic mass 79.41. It exists in three forms: yellow, grey, and black. The yellow form, comparable to white phosphorus, is less stable than the other forms and is converted into the grey (metallic) form by heat. The black form is more stable than the yellow form but is metastable with respect to the grey form. Arsenic is required in trace amounts by some organisms, but generally it acts as an antimetabolite.

arsenical **1** of or containing arsenic. **2** a drug or other agent (e.g. an insecticide, rodenticide, or nerve gas) containing arsenic as an active principle.

artemesinin *see* **sesquiterpene lactone**.

arteriosclerosis a pathological condition in which there is a thickening and loss of elasticity of the walls of the arteries, which may become calcified. This interferes with the blood supply to various organs and tissues, resulting in impaired function. It normally, though not invariably, results from **atherosclerosis**.

Arthus reaction a **complement**-dependent hypersensitivity reaction caused when antigen reacts with precipitating antibody in the skin or other tissues, forming microprecipitates in and around the small blood vessels and, secondarily, damaging cells. In the **passive Arthus reaction** antibody is injected intravenously and the antigen applied locally; in the **reversed passive Arthus reaction** the opposite applies. An **active Arthus reaction** may occur when antigen is injected locally subsequent to previous injection of the same antigen. The inflammation that results is by type III mechanisms (*see* **hypersensitivity** (def. 2)). [Described by (Nicholas) Maurice Arthus (1862–1945), French physiologist and bacteriologist, in 1903.]

articulin any of a family of cytoskeletal proteins of the **epiplasm** of flagellate and ciliate organisms. They form filaments and larger sheets or tubes. They contain repeated valine- and proline-rich motifs with the consensus VPVP_ _V_ _ _V.

aryl any univalent organic radical derived from an **arene** by loss of one hydrogen atom.

arylene any bivalent organic group derived from an **arene** by loss of two hydrogen atoms.

arylsulfatase any of a group of enzymes that catalyse the hydrolysis of a phenol sulfate to a phenol and sulfate. Example from *Escherichia coli*: database code ASLA_ECOLI, 551 amino acids (60.65 kDa). Arylsulfatases A, B, and C are com-

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mon names for **cerebroside-sulfatase**, ***N*-acetylgalactosamine-4-sulfatase**, and **steryl-sulfatase** respectively.

As *symbol for* arsenic.

ASA dehydrogenase *see* **aspartate-semialdehyde dehydrogenase**.

ASAT *(in clinical biochemistry) abbr. for* aspartate aminotransferase. *See* **aspartate transaminase**.

AS-C *abbr. for* Achaete–Scute complex. *See also* **AS-C protein**.

ascarylose 3,6-dideoxy-L-mannose; 3,6-dideoxy-L-*arabino*-hexose; a component of glycolipids found in eggs of the nematode, *Ascaris*, and in the bacterium, *Yersinia pseudotuberculosis*, type V. For the D enantiomer *see* **tyvelose**.

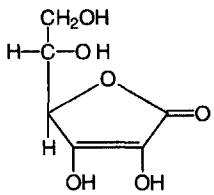
ascending boundary the solute boundary that moves upwards in one arm of the cell during electrophoresis in a **Tiselius apparatus**.

ascending chromatography any of the techniques of **chromatography** in which the mobile phase moves upwards over the solid phase.

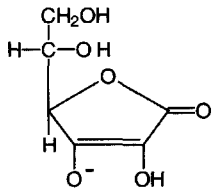
ascites the accumulation of serous fluid in the peritoneal cavity. The presence of ascites may be due to the growth of a tumour elsewhere in the body, the ascitic fluid then containing a suspension of single tumour cells. Administration of a **hybridoma** results in the formation of **monoclonal antibodies** which can be recovered from the ascitic fluid. —**ascitic** *adj.*

Ascoli test a precipitin test used in the serological diagnosis of anthrax. The antigens are extracted with boiling saline and detected by a ring test with immune serum.

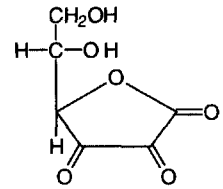
ascorbic acid a carbohydrate-like compound, containing six carbon atoms per molecule, the L enantiomer of which is found in fruit and vegetables. It has vitamin C activity in humans (most other primates can synthesize ascorbic acid) and guinea pigs. Humans are among the few higher animals that are unable to synthesize L-ascorbic acid, owing to a deficiency of **L-gulonolactone oxidase**, the enzyme catalysing the terminal step in L-ascorbic acid synthesis. The molecule contains an ene-diol group, one hydroxyl group of which is acidic (pK_a 4.04) and ionizes to give an anion ascorbate; the other ene-diol hydroxyl acts as a reducing group ($E^{o\prime}$ = +0.058 V, pH 7), and is oxidized on conversion to dehydroascorbate. Ascorbate is required together with ferric ion as a cofactor in the oxidation of prolyl residues in collagen to hydroxyprolyl residues and in other reactions.



ascorbic acid



ascorbate ion



dehydroascorbic acid

ascospore a (usually sexually derived) haploid spore formed within an **ascus**.

AS-C protein *abbr. for* Achaete–Scute complex protein; any of a family of proteins encoded by the Achaete–Scute complex, a gene cluster first discovered in *Drosophila* but with analogues in mammals and other organisms. They are involved in the determination of the neuronal precursors in the peripheral and central nervous systems. The T3, T4, and T5 proteins label strongly in the presumptive stomatogastric nervous system, while T8 is more prominent in the presumptive procephalic lobe. They resemble other members of the **MYC** family of helix-turn-helix transcription factors. Example, AS-C protein T4 (*Drosophila melanogaster*): database code AST4_DROME, 345 amino acids (38.08 kDa).

ascus (*pl.* **asci**) a sac-like fruiting body formed in ascomycete fungi, e.g. yeasts and *Neurospora*; it contains (typically eight) **ascospores** when mature.

+ase *suffix* denoting an enzyme; it is generally attached to a root indicating the substrate and/or the nature of the reaction catalysed. [From **diastase**.]

asemantic molecule any molecule that is not produced by an organism and therefore does not express any of the information that the organism contains. Absorbed molecules, although not derived from information contained within the organism, may nevertheless offer information about the organism relating to its absorption mechanisms. *See* **semantide**. *See also* **episemantic molecule**.

asepsis 1 the state of being **aseptic**. 2 the methods of making or keeping something aseptic. *Compare* **antisepsis**.

aseptic sterile; free from pathogenic microorganisms. *Compare* **antiseptic** (def. 2).

aseptic technique any technique incorporating measures that prevent the contamination of cultures, sterile media, etc. and/or the inappropriate infection of persons, animals or plants, by extraneous microorganisms.

asexual reproduction *or* **agamic reproduction** the development of a new individual from either a single cell or a group of cells without any sexual process. The term includes **agamogeny** and **vegetative reproduction**.

Ash protein *another name for* **Grb2**.

asialo+ *comb. form* denoting the absence from a compound of sialic-acid residues, e.g. after their deliberate enzymic removal from a naturally occurring **sialo-** (def. 2) compound.

A side the side of the nicotinamide ring of NAD(P)H from which projects the *pro-R* hydrogen atom (known as H_A) at the 4 position. *Compare* **B side**. *See also* ***pro-R*,*pro-S* convention**.

A site *abbr. for* aminoacyl-tRNA site (of a ribosome).

Asn *symbol for* a residue of the α-amino acid L-asparagine (alternative to N).

AsnC the asparagine biosynthetic operon regulatory protein, the product of *asnC*. In *Escherichia coli* it is the activator of *asnA* expression, the autogenous regulator of *asnC* expression, and the repressor of *gidA* (a gene of *E. coli* associated with glucose-inhibiting division) at the post-transcriptional level. It is a **helix-turn-helix** (HTH) protein and the prototype for AsnC HTH family of regulatory proteins; database code ASNC_ECOLI, 152 amino acids (16.87 kDa).

ASO *abbr. for* antistreptolysin-O; *see* **streptolysin**.

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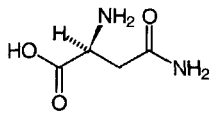
Asp *symbol for* a residue of the α-amino acid L-aspartic acid (alternative to D).

asparaginase EC 3.5.1.1; *other names*: L-asparaginase; *systematic name*: L-asparagine amidohydrolase; an enzyme that catalyses the hydrolysis of L-asparagine to L-aspartate and NH_3. It is an effective antileukemic drug when injected into the bloodstream, its action being to deprive fast-growing tumour cells of the exogenous asparagine they require for rapid growth. Its clinical usefulness is limited because it causes damage to tissues with low asparagine synthetase activity. Several isoenzymes are found in several bacteria. Example, L-asparaginase I from *Escherichia coli*, a homotetramer: database code ASG1_ECOLI, 338 amino acids (37.08 kDa).

asparaginate **1** asparagine anion; the anion, $H_2N–CO–CH_2–CH(NH_2)–COO^-$, derived from asparagine. **2** any salt containing the asparagine anion. **3** any ester of asparagine.

asparagine *trivial name for* the β-amide of aspartic acid: aspartic 4-amide; α-aminosuccinamic acid; 2-amino-3-carbamoylpropanoic acid, $H_2N–CO–CH_2–CH(NH_2)–COOH$; a chiral α-amino acid. L-Asparagine (*symbol*: A *or* Asn; *(formerly) also* Asp(NH_2)), (*S*)-2-amino-3-carbamoylpropanoic acid, is a coded amino acid found in peptide linkage in proteins; codon: AAC or AAU. It is a nonessential dietary amino acid in mammals and is glucogenic. One residue per molecule of D-asparagine (*symbol*: D-Asn *or* DAsn), (*R*)-2-amino-3-carbamoylpropanoic acid, may occur in the antibiotic bacitracin A as an alternative to one of D-aspartic acid. *Compare* **isoasparagine**.



L-asparagine

asparagine synthase (glutamine-hydrolysing) EC 6.3.5.4; *other name*: asparagine synthetase (glutamine-hydrolysing). An enzyme that catalyses a reaction between ATP, L-aspartate, and L-glutamine to form AMP, pyrophosphate, L-asparagine, and L-glutamate. Example from asparagus: database code ASN1_ASPOF, 589 amino acids (65.97 kDa); it contains a glutamine amidotransferase motif. *Compare* **aspartate–ammonia ligase**.

asparagino **1** N^2-asparagino; the alkylamino group, $H_2N–CO–CH_2–CH(COOH)–NH–$, derived from asparagine by loss of a hydrogen atom from its α-amino group. **2** N^4-asparagino; the acylamino group, $H_2N–CH(COOH)–CH_2–CO–NH–$, derived from asparagine by loss of a hydrogen atom from its amide group.

asparaginyl the acyl group, $H_2N–CO–CH_2–CH(NH_2)–CO–$, derived from asparagine. *Compare* **isoasparaginyl**.

aspartame *N*-L-α-aspartyl-L-phenylalanine methyl ester; a low-calorie artificial sweetener, about 160 times sweeter than sucrose in aqueous solution. Its sweetness is lost in cooking due to hydrolysis of the methyl ester. It is to be avoided in patients with phenylketonuria.

aspartase EC 4.3.1.1; *recommended name*: aspartate ammonia-lyase; *other name*: fumaric aminase. An enzyme that catalyses the hydrolysis of L-aspartate to fumarate and NH_3. Example from *Escherichia coli*, homotetramer: database code ASPA_ECOLI, 478 amino acids (52.30 kDa).

aspartate **1** aspartate(1–) *or* hydrogen aspartate; the monoanion derived from aspartic acid. In theory, the term denotes any ion or mixture of ions formed from aspartic acid and having a net charge of –1, although the species $^-OOC–CH_2–CH(NH_3^+)–COO^-$ generally predominates in practice. **2** *the systematic name for* aspartate(2–); the dianion derived from aspartic acid. **3** any salt containing an anion of aspartic acid. **4** any ester of aspartic acid.

aspartate aminotransferase *see* **aspartate transaminase**.

aspartate–ammonia ligase EC 6.3.1.1; *other name*: asparagine synthetase; an enzyme that catalyses the reaction of ATP with L-aspartate and NH_3 to form AMP, pyrophosphate, and L-asparagine. Example from *Escherichia coli*: database code ASNA_ECOLI, 330 amino acids (36.61 kDa). *Compare* **asparagine synthase (glutamine-hydrolysing)**.

aspartate carbamoyltransferase *see* **aspartate transcarbamylase**.

aspartate kinase EC 2.7.2.4; *other name*: aspartokinase; an enzyme that catalyses the formation of 4-phospho-L-aspartate from ATP and L-aspartate with release of ADP. The reaction is the first step in the biosynthesis of lysine, methionine, and threonine in plants and bacteria. In *Escherichia coli*, the pathway for the synthesis of each amino acid is independently controlled by regulation of isoenzymes specific for each pathway. Example from yeast: database code AK_YEAST, 527 amino acids (58.04 kDa). *See* **homoserine dehydrogenase** for another example.

aspartate-semialdehyde dehydrogenase EC 1.2.1.11; *systematic name*: L-aspartate-4-semialdehyde:$NADP^+$ oxidoreductase (phosphorylating); *other name*: ASA dehydrogenase; an enzyme that, although reversible, normally catalyses the formation of L-aspartate-4-semialdehyde, orthophosphate, and $NADP^+$ from L-4-aspartylphosphate and NADPH. Its product is a component of a pathway involved in the biosynthesis of lysine and methionine, and can be converted either into dihydropicolinate (a precursor of lysine) or into homoserine (a precursor of methionine). Example from *Escherichia coli*: DHAS_ECOLI, 367 amino acids (39.97 kDa).

aspartate transaminase *abbr. (in clinical biochemistry)*: AST; EC 2.6.1.1; *systematic name*: L-aspartate:2-oxoglutarate aminotransferase; *other names*: transaminase A; glutamic–oxaloacetic transaminase; glutamic–aspartic transaminase. An enzyme that catalyses a reaction between L-aspartate and 2-oxoglutarate to form oxaloacetate and L-glutamate. It is a pyridoxal-phosphate enzyme, very widely distributed, performing a pivotal role in amino-acid metabolism. In mammals this includes the transfer of amino groups to aspartate, which then transfers them into the **urea cycle** through **argininosuccinate synthase**. Very high plasma concentrations of AST (more than 100 times normal) are found in cases of severe tissue damage including acute hepatitis, crush injuries, and tissue hypoxemia. In jaundice and myocardial infarction the levels reach 10 to 20 times normal; in myocardial infarction AST starts to rise about 12 h after the infarct, reaching a peak at 24 to 36 h, then declining over 2 to 3 days. The normal level in human plasma is in the range 10–50 IU L^{-1} (method-dependent; assumed presence of vitamin B_6 in the assay). Examples: (1) mitochondrial enzyme, homodimer: database code (precursor) AATM_HUMAN, 430 amino acids (47.42 kDa); (2) cytoplasmic isoform, homodimer: database code AATC_HUMAN, 412 amino acids (46.08 kDa).

aspartate transcarbamylase *abbr.*: ATCase; EC 2.1.3.2; *recommended name*: aspartate carbamoyltransferase; *other names*: carbamylaspartotranskinase. An enzyme that catalyses a reaction between carbamoyl phosphate and L-aspartate to form *N*-carbamoyl-L-aspartate with release of orthophosphate. In many eukaryotes it is an activity of the **CAD protein**. In *Escherichia coli*, operon *pyrBI* codes for catalytic and regulatory chains; database code ECOPYRBI, catalytic chain 311 amino acids (34.37 kDa). There are six motifs and the 3-D structure of the enzyme in several states is known, e.g. database code NRL_1AT1A. The protein has a very high α-helical content. Carbamoyl aspartate is an important component of the pathway for *de novo* synthesis of pyrimidines.

aspartic denoting a residue of aspartic acid, whether or not the β-carboxyl group is protonated.

aspartic acid *trivial name for* α-aminosuccinic acid; 2-aminobutanedioic acid, $HOOC–CH_2–CH(NH_2)–COOH$; a chiral α-amino acid. L-Aspartic acid (*symbol*: D *or* Asp), (*S*)-

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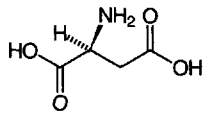
2-aminobutanedioic acid, is a coded amino acid found in peptide linkage in proteins; codon: GAC *or* GAU. In mammals it is a nonessential dietary amino acid and is glucogenic. Residues of D-aspartic acid (*symbol*: D-Asp *or* DAsp), (*R*)-2-aminobutanedioic acid, are found in the cell-wall material of bacteria of various species, and one residue per molecule may occur in the antibiotic bacitracin A as an alternative to one of D-asparagine. It is also formed by racemization of L-aspartic acid residues in long-lived proteins such as crystallins, dentine, and myelin.



L-aspartic acid

aspartic amide 1 aspartic 1-amide; *an alternative name for* **isoasparagine**. 2 aspartic 4-amide; *an alternative name for* **asparagine**.

aspartic endopeptidase *or (formerly)* **acid proteinase** *or* **aspartyl protease** *or* **carboxyl protease** any enzyme of the sub-subclass EC 3.4.23, comprising endopeptidases having a pH optimum below 5 by virtue of an aspartic residue being involved in the catalytic process. The group includes cathepsin D, chymosin, the pepsins, and renin.

asparto the alkylamino group, HOOC–CH_2–CH(COOH)–NH–, derived from aspartic acid.

aspartoacylase *see* **aminoacylase**.

aspartokinase *see* **aspartate kinase**; *see also* **aspartokinase/homoserine dehydrogenase**.

aspartokinase/homoserine dehydrogenase a multifunction enzyme, characterized in *Escherichia coli*, that catalyses two steps in the pathway from aspartate to diaminopimelate and lysine, to methionine, and to threonine and isoleucine. It is allosterically regulated by threonine. Example from *E. coli*: database code AK1H_ECOLI, 820 amino acids (89.02 kDa); homotetramer; the first 149 amino acids form the aspartokinase domain, while the last 350 residues form the homoserine dehydrogenase domain.

aspartoyl the diacyl group, –CO–CH_2–CH(NH_2)–CO–, derived from aspartic acid.

α-aspartyl aspart-1-yl; the α-monoacyl group, HOOC–CH_2–CH(NH_2)–CO–, derived from aspartic acid.

β-aspartyl *or (formerly)* **isoaspartyl** aspart-4-yl; the β-monoacyl group, HOOC–CH(NH_2)–CH_2–CO–, derived from aspartic acid.

β-aspartyl-*N*-acetylglucosaminidase EC 3.2.2.11; *systematic name*: 1-β-aspartyl-*N*-acetyl-D-glucosaminylamine L-asparaginohydrolase. An enzyme that catalyses the hydrolysis of 1-β-aspartyl-*N*-acetyl-D-glucosaminylamine to *N*-acetyl-D-glucosamine and L-asparagine. Example from *Flavobacterium meningosepticum*: database code A42259, 339 amino acids (37.16 kDa). *See also* **aspartylglucosaminuria**.

aspartylglucosaminuria a metabolic disorder with autosomal recessive inheritance; it results in progressive mental retardation due to lysosomal accumulation of aspartylglucosamine (2-acetamido-1-β-L-aspartamido-1,2-dideoxy-β-D-glucose), which is excreted in abnormally high amounts in the urine. This compound is commonly found in several glycoproteins in normal individuals. The first sign of the condition is usually a delay in speech development (1–4 years). The enzymic effect is a deficiency of lysosomal aspartylglucosaminidase (N^4-(β-*N*-acetylglucosaminyl)-L-asparaginase, EC 3.5.1.26).

aspartylglucosylamine deaspartylase *see* **N^4-(β-*N*-acetylglucosaminyl)-L-asparaginase**.

β-aspartyl phosphate *or* **4-phospho-L-aspartate** *or* **aspartyl-β-phosphate** an intermediate in the biosynthesis of lysine, threonine, and methionine in bacteria and plants. It is formed by **aspartate kinase**. It is converted to β-aspartyl semi-aldehyde, which is converted by the action of **homoserine dehydrogenase** to homoserine, a precursor of threonine or methionine. Alternatively addition of pyruvate to β-aspartyl phosphate leads to formation of dihydropicolinate, a precursor of lysine. A β-aspartyl phosphate residue is formed by phosphorylation of an aspartyl residue of Na^+,K^+-ATPase during the transport process.

aspartyl protease *an older name for* **aspartic proteinase**.

β-aspartyl semi-aldehyde OHC–CH_2–CH(NH_2)–COOH; *see* **β-aspartyl phosphate**.

aspartyl shift *or* **α → β-aspartyl shift** an intramolecular rearrangement reaction involving aspartic-acid residues that can occur during chemical synthesis or degradation of peptides. The β-carboxyl group of an aspartic residue displaces the α-carboxyl of the same residue from its amide (= peptide) linkage to the amino group of the adjacent amino-acid residue, thus forming an acid-sensitive β-amide (= isopeptide) linkage. Conditions must favour ionization of the β-carboxyl group. The reaction may be used to advantage in the partial hydrolysis of polypeptides and proteins by very dilute acid, but may occur to disadvantage during base-catalysed hydrolytic removal of protecting groups in the course of peptide synthesis.

Aspergillus a genus of filamentous fungi containing species of industrial and genetic importance. *A. niger* and *A. oryzae* are used in the production of citric acid, industrial enzymes, and fermented foods. The sexual species *A. nidulans* has been an important research tool in both biochemical and mitochondrial genetics. *A. flavus* is a source of **aflatoxins**.

asperlicin a naturally occurring antagonist of the peptide **cholecystokinin**, produced by various strains of *Aspergillus alliaceus*.

aspirin *or* **acetylsalicylic acid** 2-(acetyloxy)benzoic acid; an irreversible inhibitor of **prostaglandin-endoperoxide synthase**, through covalent acetylation of the α-amino group on the terminal serine active site. It is used as a drug for its antithrombotic activity and nonsteroidal anti-inflammatory and associated actions (antipyrexia, analgesia). *See also* **salicylic acid**.

Asp(NH_2) *(formerly) symbol for* L-asparagine.

Asp-NH_2 *symbol for* L-isoasparagine, an α-amino acid.

Asp(OMe) *symbol for* β-methyl aspartate; O^4-methyl hydrogen aspartate.

Asp-OMe *symbol for* α-methyl aspartate; O^1-methyl hydrogen aspartate.

assay *n.* 1 the determination of the activity, potency, strength, etc. of a substance, either on an absolute basis or in comparison with that of a standard preparation. 2 the determination of the relative amount(s) of one or more components of a mixture, or of the degree of purity of a substance. 3 to carry out such a determination. *See also* **bioassay**, **immunoassay**, **microbiological assay**, **radioassay**.

assimilation the absorption of simple foodstuffs (or of the products of their digestion) and their use in the biosynthesis of complex constituents of the organism; sometimes restricted to **photosynthesis**. —**assimilatory** *adj.*

assimilatory nitrate reduction *see* **nitrate reduction**.

assimilatory regulatory protein a *abbr.*: ARP_a; *obsolete name for* ferredoxin–thioredoxin reductase, obtained from chloroplasts.

assimilatory regulatory protein b *abbr.*: ARP_b; *obsolete name for* thioredoxin, obtained from chloroplasts.

association a reversible union between two chemical entities, whether alike or different, to form a more complex substance. *Compare* **dissociation** (def. 1).

association constant *symbol*: K_{ass} *or* K_a; the **equilibrium constant** for the reversible formation of a complex chemical compound from two or more simpler entities; the reciprocal of the **dissociation constant**, K_{diss}. Sometimes an **apparent** association

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constant, K'_{ass}, constrained with respect to stated values of certain variables (e.g. pH), is determined (*see* **equilibrium constant**). For an association of the type: A + B AB the (concentration) association constant is given by:

$$K_{ass} = [AB]/([A] \times [B]) = 1/K_{diss}$$

See also **affinity constant, off-rate, on-rate, stability constant.**

assortment *or* **reassortment** during meiosis, the distribution to opposing cell poles of the two members of each pair of chromosomes at anaphase I and of the two members of each pair of chromatids at anaphase II.

AST *(in clinical biochemistry) abbr. for* aspartate transaminase.

astacin EC 3.4.24.21; *other name*: *Astacus* proteinase; crayfish small-molecule proteinase; an enzyme that catalyses the hydrolysis of peptide bonds in substrates containing five or more amino acids, preferentially with Ala in the P1′ and Pro in the P2′ positions (*see* **peptidase P-sites**). Zinc is a cofactor. Example, including 3-D structure, from the European fresh water crayfish: database code NRL_1AST, 200 amino acids (22.58 kDa).

astatin any of a subfamily of zinc metalloendopeptidases of unallocated number within sub-subclass EC 3.4.24, including **tolloid** (*Drosophila*) and **bone morphogenetic protein 1** (human), involved in differentiation.

astatine *symbol*: At; a halogen element of group 17 of the IUPAC **periodic table**; atomic number 85. It occurs as short-lived isotopes of mass numbers 215, 216, and 218 resulting from β-decay of other radioactive elements. Astatine-211, an α-emitter of half-life 7.5 h, results from α-bombardment of bismuth; it has potential in radiotherapy.

astaxanthin 3,3′-dihydroxy-*β*,*β*-carotene-4,4′-dione; a carotenoid pigment found mainly in animals (e.g. crustaceans, echinoderms) but also occurring in plants. It can occur free (as a red pigment), as an ester (e.g. the dipalmitate), or as a blue, brown, or green chromoprotein.

Aston, Francis William (1877–1945), British experimental physicist; Nobel Laureate in Chemistry (1922) 'for his discovery, by means of his mass spectrograph, of isotopes in a large number of non-radioactive elements, and for his enunciation of the whole-number rule'.

astral microtubule *see* **prometaphase.**

Astrup technique a micro technique for the rapid determination of the acid–base status of a sample of blood. The pH of the blood as taken is measured and the remainder of the sample split into two and each part equilibrated with a different CO_2/O_2 mixture of known $p(CO_2)$ and their pH values measured. These last two pH values and the corresponding $p(CO_2)$ values are plotted on a **Siggaard–Andersen nomogram** and the points joined by a straight line. The $p(CO_2)$ of the original sample may be obtained from the point on this line corresponding to the pH of the blood as taken. Furthermore, the **standard bicarbonate value** of the blood may be obtained from the point where the straight line intersects with a scale on the $p(CO_2)$ axis at 5.33 kPa (40 mmHg).

ASV *abbr. for* anodic stripping voltammetry.

Asx *symbol for* a residue of either of the *α*-amino acids L-aspartic acid or L-asparagine when the state of amidation is uncertain (alternative to B).

asymmetric synthesis any synthesis of a compound that produces only one of two possible enantiomers of the product. This is usually the case for enzymic but not for nonenzymic reactions.

asymmetry absence of **symmetry**. A particular example of its meaning in biochemistry relates to the different phospholipid composition of the inner and outer leaflets of a lipid bilayer, said to confer asymmetry of composition. **—asymmetric** *adj.*

asymmetry potential the usually small potential across a membrane electrode, such as a glass electrode, when both sides are immersed in identical solutions. It is probably due to slight imperfections in the membrane.

asynapsis absence of **synapsis** (def. 1); i.e. the failure of homologous chromosomes to pair during meiosis.

At *symbol for* astatine.

atactic characterized by or showing irregularity in the spatial arrangement of the parts of a molecule.

atactic polymer any regular polymer in which the molecules display essential randomness with regard to the configurations at all main-chain sites of steric isomerism.

+ate *suffix* **1** designating any anion (including mixtures of anion and free acid), salt, or ester of any **oxoacid** (def. 1) other than an +ous acid. **2** denoting the product of a process, e.g. distillate, hydrolysate.

ATF *abbr. for* activating (or activator) transcription factor; any of various transcription factors for eukaryotic RNA polymerase II promoters that bind to **CRE**. Example, ATF-A and ATF-A-δ (human): these form a dimer; they have different sequences (amino acids 114–134 missing in δ), and possess a leucine zipper; database code ATFA_HUMAN, 483 amino acids (54.70 kDa).

(A + T)/(G + C) ratio the ratio of the sum of the adenine plus thymine bases to the sum of the guanine plus cytosine bases in a DNA molecule or preparation. The ratio is to some extent a characteristic of an individual type of DNA molecule. *Compare* **Chargaff's rules**.

athero-ELAMs endothelial leukocyte-adhesion molecules, i.e. **selectins**, expressed in atherosclerotic plaques.

atheroma a condition or process affecting blood vessels in which plaques form beneath the intima (i.e. inner lining). These start as infiltration by lipid-containing cells but later become invaded by fibrous tissue or become calcified. It is associated with hypercholesterolemia and defects in the **apolipoprotein B receptor** **—atheromatous** *adj.*

atherosclerosis a degenerative condition affecting arteries in which there is hyperplasia of the outer coat and fatty degeneration of the middle coat of the arteries due to **atheroma**.

aThr *symbol for* a residue of the *α*-amino acid L-allothreonine, (2*S*,3*S*)-2-amino-3-hydroxybutanoic acid.

atmosphere **1** the envelope of gas surrounding the Earth. **2** any local gaseous environment. **3** *symbol*: atm; a non-SI unit of pressure equal to 101.325 kPa; the pressure that will support a column of mercury 760 mm high at 273.15 K, sea-level, and latitude 45°.

atom a unit of matter consisting of a single **nucleus** surrounded by one or more orbital **electrons**. The number of electrons is normally sufficient to make the atom electrically neutral; adding or removing electrons converts the atom into a negative or positive ion, but this is regarded as a state of the same atom since the atom is characterized by its nucleus.

atomic absorption spectrophotometry a quantitative version of **atomic absorption spectroscopy** in which the absorption of electromagnetic radiation by the ground-state atoms in the flame is measured photoelectrically and the concentration of the element in question calculated by reference to the absorption observed with solutions of the elements of known concentration.

atomic absorption spectroscopy an analytical technique, based on the observation of the absorption of light energy by atoms, in which an atomic vapour of an element is formed by aspiration of a solution of the element into a flame, or otherwise, so that the large majority of the element's atoms remain in the non-emitting ground state. These ground-state atoms absorb electromagnetic radiation of their own specific resonance frequency, to an extent that is proportional to the density of the elemental atoms in the flame.

atomic mass constant *symbol*: m_u; a fundamental constant equal to the mass of a carbon-12 atom divided by 12; it is equal to the **unified atomic mass unit**.

atomic mass unit *abbr. (formerly)*: amu; *see* **unified atomic mass unit.**

atomic number *an older alternative name for* **proton number.**

atomic orbital the volume containing all the points within a

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free atom at which the Schrödinger wave-function of an electron is of appreciable magnitude.

atomic radius the distance between the centre of the nucleus and the outermost electron shell of an atom. *Compare* **van der Waals radius**.

atomic weight *abbr.*: at. wt.; *former name for* **relative atomic mass**.

atomic weight unit *abbr.*: awu; one-twelfth of the mean mass of the neutral atoms of naturally occurring carbon.

atomizer *or* **atomiser** an instrument for breaking up a solution into a spray of fine droplets.

atom percent the proportion of any nuclide in a mixture expressed as a numerical percentage of all the atoms of that element present irrespective of their nuclidic masses.

atom percent excess a measure of the abundance of a stable nuclide in a sample expressed in terms of the excess, in **atom percent**, over that naturally present. It is used to express the extent of enrichment or dilution of substances labelled with stable isotopes.

atopy *or* **atopic allergy** the tendency of some individuals to develop immediate hypersensitivity reactions to **allergens**. It is probably hereditary.

ATP *abbr. for* adenosine 5′-triphosphate.

ATPase *abbr. for* adenosine triphosphatase.

ATP-diphosphatase *see* **apyrase**.

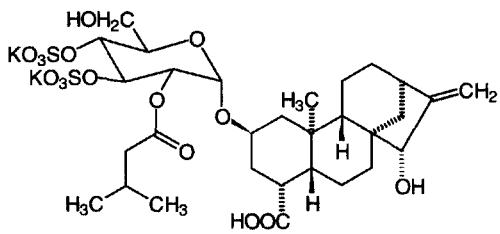
ATP[α,β-CH$_2$] *abbr. for* α,β-methyleneadenosine 5′-triphosphate; i.e. adenosine 5′-[α,β-methylene]triphosphate.

ATP[β,γ-CH$_2$] *abbr. for* β,γ-methyleneadenosine 5′-triphosphate; i.e. adenosine 5′-[β,γ-methylene]triphosphate.

ATP[β,γ-NH] *abbr. for* β,γ-imidoadenosine 5′-triphosphate; i.e. adenosine 5′-[β,γ-imido]triphosphate.

ATP(S) *abbr. for* adenosine 5′-γ-thiotriphosphate.

ATP synthetase *see* **H$^+$-transporting ATP synthase**.



atractyloside

atractyloside an extremely toxic glycoside, obtained from the rhizomes of the Mediterranean thistle *Atractylis gummifera*, that produces hypoglycemia and convulsions in animals. It inhibits oxidative phosphorylation, in particular the translocation of mitochondrial adenine nucleotides. Carrier-bound adenine nucleotides are apparently replaced by atractyloside owing to the latter's higher affinity for a common translocation site. *Compare* **bongkrekic acid**.

A-transferase EC 2.4.1.40; *recommended name*: fucosylgalactose α-*N*-acetylgalactosaminyltransferase; *other names*: fucosylglycoprotein α-*N*-acetylgalactosaminyltransferase, [histo-blood group] A-transferase; an enzyme that can catalyse a reaction between UDP-*N*-acetyl-D-galactosamine and glycoprotein α-L-fucosyl-(1,2)-D-galactose to form UDP and glycoprotein *N*-acetyl-α-D-galactosaminyl-(1,3)-[L-fucosyl-(1,2)]-D-galactose. It thus catalyses the addition of *N*-acetylgalactosamine to the H antigen of the **ABH antigen** system, forming the A antigen. This and the **B-transferase** protein are products of alleles of the *ABO* gene, differing in only four residues.

atrial of or pertaining to an **atrium**.

atrial natriuretic peptide *see* **natriuretic peptide**.

atrial natriuretic peptide receptor *see* **natriuretic peptide receptor**.

atrioactivase a specific serine protease, present in bovine cardiac atria, that catalyses processing of the precursor of **natriuretic peptide** by selective cleavage at Arg^{89}.

atriopeptins biologically active peptides isolated from mammalian cardiac atria. Atriopeptin I (I) has 21 amino acids, with the structure

SSCFGGRIDRIGAQSGLGCNS

(3–19 disulfide link); atriopeptin II (II) is the same with additional Phe-Arg residues at the C terminus; atriopeptin III is the same as II but with an additional Tyr residue at the C terminus. I relaxes intestinal smooth muscle but not vascular smooth muscle, while II relaxes both. *Compare* **natriuretic peptide**.

atrium (*pl.* **atria**) *or (formerly)* **auricle** **1** either of the two chambers of the heart that lie above the ventricles. They receive blood from the afferent veins and pump it into the ventricles. **2** any of various anatomical chambers that receive the openings of other cavities.

atrolysin B EC 3.4.24.41; *other names*: *Crotalus atrox* metalloendopeptidase B; hemorrhagic toxin B (*abbr.*: HT-B); a snake-venom enzyme that catalyses the cleavage of His^5-|-Leu^6, His^{10}-|-Leu^{11}, Ala^{14}-|-Leu^{15}, Tyr^{16}-|-Leu^{17}, and Gly^{23}-|-Phe^{24} of the insulin B-chain. The reaction is identical to the cleavage of insulin B-chain by **atrolysin C**. The enzyme also cleaves Ser-|-Xaa bonds in glucagon. It is a zinc-requiring enzyme.

atrolysin C EC 3.4.24.42; *other names*: *Crotalus atrox* metalloendopeptidase C; hemorrhagic toxin C and D; a snake-venom enzyme that catalyses the cleavage of His^5-|-Leu^6, His^{10}-|-Leu^{11}, Ala^{14}-|-Leu^{15}, Tyr^{16}-|-Leu^{17}, and Gly^{23}-|-Phe^{24} of the insulin B-chain. With small-molecule substrates it prefers hydrophobic residues at the P2′ position and small residues such as Ala or Gly at the P1 position (*see* **peptidase P-sites**). It is a zinc-requiring enzyme. Example from *C. atrox* (the Western diamondback rattlesnake): database code HRTD_CROAT, 203 amino acids (23.22 kDa).

atrolysin E EC 3.4.24.44; *other names*: *Crotalus atrox* metalloendopeptidase E; hemorrhagic toxin E; a snake-venom enzyme that catalyses the cleavage of Asn^3-|-Gln^4, Ser^9-|-His^{10}, and Ala^{14}-|-Leu^{15} bonds in the insulin B-chain and Tyr^4-|-Gln^5 and Ala^8-|-Ser^9 in the A chain. It cleaves type IV collagen at Ala^{258}-|-Gln^{259} in α_1-collagen and at Gly^{191}-|-Leu^{192} in α_2-collagen. It is a zinc-requiring enzyme. Example from *C. atrox* (the Western diamondback rattlesnake): database code HRTE_CROAT, 478 amino acids (53.58 kDa).

atrolysin F EC 3.4.24.45; *other names*: *Crotalus atrox* metalloendopeptidase F; hemorrhagic toxin F; a snake-venom enzyme that catalyses the cleavage of Val^2-|-Asn^3, Gln^4-|-His^5, Leu^6-|-Cys^7, His^{10}-|-Leu^{11}, Ala^{14}-|-Leu^{15}, and Tyr^{16}-|-Leu^{17} bonds in the insulin B-chain. It is a zinc-requiring enzyme.

atrophy diminution in the size of a tissue or organ after full normal development has been attained. It is often a result of nutritional deficiency and/or decreased functional activity.

atropine (±)-hyoscyamine; tropyl DL-tropate; 1αH,5αH-tropan-3-ol (±)-tropate a tropane alkaloid obtained from deadly nightshade, *Atropa belladonna*; and other Solanaceae. The racemic mixture is a tertiary ammonium compound that acts as a **muscarinic receptor** antagonist. It is used as an anticholinergic, mydriatic, etc. *See also* **hyoscine**.

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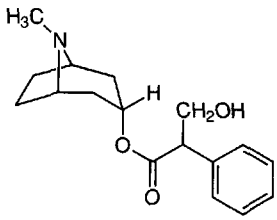

atropine

attachment proteins *general term for* proteins that are involved in binding other proteins to cell structures, e.g. **vinculin**, or α-actinin (*see* **actinin**), which bind actin to the plasma membrane.

attachment site *see* **active site** (def. 2).

A–T tailing **homopolymer tailing** of two types of duplex DNA molecule or fragment by the successive addition of adenine deoxynucleotide residues (A) to the 3′ ends of molecules of one type and the complementary addition of thymine deoxynucleotide residues (T) to the 3′ ends of molecules of the second type.

attenuance *symbol*: *D*; the logarithm to the base 10 of the ratio of the **radiant powers** of the incident radiation, P_0, and the transmitted radiation, P; thus:

$$D = \lg(P_0/P) = \lg T^{-1},$$

where T is the **transmittance**. Attenuance reduces to **absorbance** if the incident beam is only either transmitted or absorbed, but not reflected or scattered.

attenuated virus a virus that has become less pathogenic following passage in culture outside its natural host, or by the use of physical or chemical means.

attenuator a sequence in DNA that is located between the **operator** and the gene for the first protein in an **operon**. It can cause transcription termination. The operon for the synthesis of **tryptophan** in bacteria is an example of an operon that contains an attenuator.

atto+ *symbol*: a; *prefix* used with SI units denoting 10^{-18} times.

attractant *or* **chemoattractant** a substance that a motile cell or organism tends to move towards; i.e. one that elicits positive **chemotaxis**. For a responsive bacterium, attractants can be either nutritive or nonmetabolizable. An example is **cytotaxin**.

Au *symbol for* gold.

AUA **1** a codon in mRNA, excluding that of mammalian mitochondria, for L-isoleucine. **2** a codon in mammalian mitochondrial mRNA for L-methionine (and for *N*-formyl-L-methionine, chain initiation, in some species).

AUC a codon in mRNA for L-isoleucine.

AUG a codon in mammalian mitochondrial mRNA, and in non-mitochondrial mRNA the only codon for L-methionine and usually for *N*-formyl-L-methionine, chain initiation.

Auger effect a process by which an orbital electron in an atom passes from an excited to a lower energy level. The X-ray so produced collides with, and ejects, another orbital electron, known as an **Auger electron**, with energy in the X-ray range. [After Pierre Victor Auger (1899–1993), French physicist.]

auracyanin a small blue copper-containing bacterial outer membrane glycoprotein (one Cu^{2+} ion per protein) that donates electrons to cytochrome c_{554}. Example from *Chloroflexus aurantiacus*: database code AUB1_CHLAU, 154 amino acids (15.53 kDa).

aureomycin 7-chlortetracycline. *See* **tetracycline**.

auriculin either of two fragments of atrial **natriuretic peptide**; auriculin A is the 4–27 and B the 4–28 fragment.

Auriculin *a proprietary name for* atrial natriuretic peptide.

aurosome an artificially induced organelle occurring in animal cells cultured in the presence of gold. It is an electron-dense lysosomal body containing gold particles.

Australia antigen *an alternative name for* hepatitis B antigen. *See* **hepatitis**.

aut+ *a variant form of* **auto+**.

autacoid any druglike principle that is produced in or can be extracted from the organs of internal secretion. Autacoids include both excitatory substances (**hormones**) and inhibitory substances (**chalones**).

auto+ *or (before a vowel)* **aut+** *comb. form* **1** self; one's own. **2** occurring within oneself or itself. **3** acting by itself; automatic; spontaneous.

autoagglutination the tendency of a suspension of bacteria or other cells to agglutinate spontaneously in a simple medium not containing an **agglutinin** or other similar reagent.

autoallergy *an alternative term for* **autoimmunity**.

autoanalyser *or (esp. US)* **autoanalyzer** any instrument for effecting analyses automatically.

autoantibody an **antibody** produced in an animal that reacts with a constituent of the animal's own tissues, which thus acts as a 'self' antigen or **autoantigen**.

autoantigen an **antigen** that is a normal constituent of an individual and has the capacity to produce an **immune response** in the same individual in certain circumstances.

autocatalysis the catalysis of a chemical or biochemical reaction by one of the reaction products. —**autocatalytic** *adj.*

autochthonous derived from that part of the body where found; native. *Compare* **autologous**.

autoclave an instrument, used for sterilizing culture media, instruments, etc., that consists of an airtight chamber which can be filled with, or surrounded by, steam at high pressure.

autocoupling hapten a reactive compound of low molecular mass that, when injected into an animal, reacts with tissue antigens to form hapten–antigen compounds. These then lead to the formation of antibodies to the **hapten**.

autocrine describing an agent that acts on the cell in which it is produced.

autofluorogram *an alternative name for* **fluorogram** (when produced by **fluorography** (def. 2)).

autofluorography *an alternative term for* **fluorography** (def. 2).

autogenesis *or* **autogeny** *an alternative term for* **abiogenesis**. —**autogenetic** *adj.*

autogenous **1** self-produced. **2** originating within, especially within one's own body.

autogenous regulation the mechanism by which a protein directly controls the expression of its own structural gene.

autograft any graft or transplant of the subject's own tissue(s).

autoimmunity *or* **autoallergy** a state of immunological reactivity against constituents of the subject's own tissues.

autoimmunization *or* **autoimmunisation** the process of inducing **autoimmunity**.

autologous derived from the same organism. *Compare* **autochthonous**.

autolysate *or (esp. US)* **autolyzate** a product of **autolysis**, e.g. a suspension of broken cells.

autolysin EC 3.5.1.28; *other name*: *N*-acetylmuramoyl-L-alanine amidase; an enzyme that catalyses the hydrolysis of the link between *N*-acetylmuramoyl residues and L-amino-acid residues in certain bacterial cell-wall glycopeptides. The enzyme is required for cell separation, cell-wall turnover, etc. Example from *Staphylococcus aureus*: database code ALYS_STAAU, 481 amino acids (53.76 kDa). *See also* **lysostaphin**.

autolysis the process of self-digestion that occurs in plant and animal tissues after death of the organism or following separation of tissue from the rest of the organism. It is due to the action of the tissue's own enzymes. —**autolytic** *adj.*

autolysosome an **autophagic vacuole**.

automutagen any **mutagen** formed in an organism as a normal or abnormal metabolic product that is mutagenic in the same organism.

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autonomic nervous system *abbr.*: ANS; those parts of the **peripheral nervous system** and **central nervous system** that govern homeostasis in vertebrates and are generally independent of voluntary control.

autonomous existing or able to exist independently; used, e.g., of a tumour cell that is free of host control or of an episome or plasmid that replicates independently of the chromosome.

autophagic vacuole an enlarged **lysosome** containing subcellular structures such as mitochondria; a secondary lysosome.

autophagosome a **phagosome** containing endogenous cellular debris. *Compare* **heterophagosome**.

autophagy a process, apparently ubiquitous among eukaryotes, by which cells digest parts of their own cytoplasm. *Compare* **heterophagy**. —**autophagic** *adj.*

autophosphorylation the phosphorylation by a protein of one of its own residues. It is important in signal transduction by growth hormone receptors (*see*, e.g., **epidermal growth factor receptor**), but occurs in the case of other proteins, e.g. **caldesmon**.

autoprothrombin I *an alternative name for* factor VII; *see* **blood coagulation**.

autoprothrombin II *an alternative name for* factor IX; *see* **blood coagulation**.

autoprothrombin IIA *an alternative name for* **protein C**.

autopsy *or* **necropsy** the examination of a dead body, commonly to determine the cause of death or the presence of disease processes; a post-mortem (examination). *Compare* **biopsy**.

autoradiogram an **autoradiograph**, especially of a chromatogram or electrophoretogram.

autoradiograph *or* **autoradiogram** the image produced by **autoradiography**.

autoradiography a method by which radioactive material can be localized in, e.g., a tissue, cell, a cell part, or molecule, or in a chromatogram or electrophoretogram. The sample containing a radioactive substance is put in direct contact with a thick layer of specially prepared photographic emulsion. The radiation emitted in the decay of the radionuclide(s) activates individual silver halide grains in the emulsion rendering them susceptible to conversion to metallic silver grains by a photographic developer. After fixation the silver grains may be located either visually or by microscopy.

autosomal of, relating to, or being an **autosome**.

autosomal disease disease that results from an abnormality affecting the **autosomes**.

autosome any **chromosome** except the **sex chromosomes**. Hence the genes carried by the autosomes show **autosomal linkage** (or **autosomal inheritance**) according to the assortment of their respective autosomes to gamete cells during meiosis. Humans have 22 pairs of autosomes in addition to a pair of sex chromosomes.

autosteric effector any **effector** that binds to, and exerts its effect at, part of or immediately adjacent to the **active site** of an **allosteric** protein. It is distinguished from an **allosteric effector** operating at a distant site.

autotroph *or* **lithotroph** any organism that requires only simple inorganic substances to fulfil its nutritional requirements and for which gaseous or dissolved carbon dioxide is the sole source of carbon for the synthesis of cellular constituents. The term often includes any microorganism for which trace amounts of certain substances, e.g. vitamins, must also be supplied. Autotrophs may be subdivided into **chemoautotrophs** (*or* chemolithotrophs) and **photoautotrophs** (*or* photolithotrophs) according, respectively, to whether they are **chemotrophs** or **phototrophs**. *Compare* **heterotroph**. —**autotrophic** *adj.*; **autotrophy** *n.*

AUU a codon in mRNA for L-isoleucine.

auxiliary amino acid any amino-acid residue in the **active site** (def. 1) of an enzyme that is more than one bond distance removed from the substrate molecule in the enzyme–substrate complex. *Compare* **contact amino acid**.

auxin any of a group of plant hormones, produced by regions of actively dividing and enlarging cells, that regulate aspects of plant growth. They include indole-3-acetic acid and indole-3-acetonitrile.

auxochrome any saturated atomic grouping (e.g. -OH, $-CH_3$, $-NH_2$, -Cl, -SH) that, when attached directly to a **chromophore**, shifts the selective absorption of light in the direction of longer wavelengths and enhances the intensity of absorption.

auxostat in industrial fermentation, a **chemostat** in which the **dilution rate** can be varied, normally in response to some parameter such as growth rate or pH, so that growth rate is more readily maximized.

auxotroph any strain of microorganism (alga, bacterium, or fungus) that differs from the **wild-type** by requiring a supply of one or more growth factors. *Compare* **prototroph**. —**auxotrophic** *adj.*

auxotrophy the condition of being an **auxotroph**.

average *an alternative term for* (arithmetic) **mean**.

average life *see* **mean life**.

average molar mass *or (formerly)* **average molecular weight** any of a series of numeric characteristics of a macromolecular system that are useful for assessing the extent of its polydispersity. The three most important are the **number-average molar mass**, M_n, the **mass-average molar mass**, M_m, and the **Z-average molar mass**, M_z. These three characteristics are given by the expressions:

$$M_n = \sum n_i M_i / \sum n_i \text{ (kg mol}^{-1}\text{)}$$

$$M_m = \sum n_i M_i^2 / \sum n_i M_i \text{ (kg mol}^{-1}\text{)}$$

$$M_z = \sum n_i M_i^3 / \sum n_i M_i^2 \text{ (kg mol}^{-1}\text{)}$$

where n_i is the amount of substance of species i and M_i is the molar mass of species i. Measurement of a **colligative property**, e.g. osmotic pressure, or end-group analysis, gives M_n; light scattering, dielectric dispersion, or fluorescence depolarization measurements give M_m; and data obtained by equilibrium ultracentrifugation will yield either M_m or M_z depending on how they are treated. For polydisperse or heterogeneous systems, $M_z > M_m > M_n$, whereas for monodisperse systems these three characteristics are equal (i.e. equal to the relative molecular mass, M_r, of the single species).

average molecular weight *former name for* **average molar mass**.

average radius of gyration *an alternative term for* **mean radius of gyration**.

average relative molecular mass *former name for* **average molar mass**.

avermectin B_1 *an alternative name for* **abamectin**.

avidin a 66 kDa glycoprotein comprising four essentially identical subunits, each of which consists of a single polypeptide chain of 128 amino-acid residues. Isolated from the white of the eggs of birds and amphibia, it binds extremely strongly to **biotin** and produces biotin deficiency when fed to experimental animals. Example from *Gallus gallus* (precursor): database code AVID_CHICK, 152 amino acids (16.77 kDa); residues 1–24 form the signal.

avidity **1** the tendency of an antibody to form more-or-less stable complexes with a (macromolecular) antigen; a measure of this tendency. **2** *an alternative term for* **affinity**.

avirulent lacking **virulence**.

avitaminosis a condition resulting from deficiency of one or more **vitamins**. The deficient vitamin may be specified, as in avitaminosis A, B, etc.

Avogadro constant *or (formerly)* **Avogadro's number** *symbol*:

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L or N_A; the number of molecular entities in one mole of any chemical species. It is a fundamental physical constant, of value 6.022 136 7(36) × 10^{23} mol^{-1}. *Compare* **Loschmidt constant**.

Avogadro number *or* **Avogadro's number** the numerical value of the **Avogadro constant**.

Avogadro's hypothesis *or* **Avogadro's law** the principle that equal volumes of all ideal gases, at the same temperature and pressure, contain equal numbers of molecules. [After Lorenzo Romano Amadeo Carlo Avogadro, Count of Quaregna and Cerreto (1776–1836), Italian physicist and chemist who formulated it in 1811.]

avogram *see* **dalton**.

AVP *abbr. for* arginine vasopressin.

axenic pertaining to the growth of organisms of a single species in the absence of living organisms or living cells of any other species (also, strictly, in the absence of living cells of the organism itself except those in the intact living organism and its gametes). —**axenity** *n.*; **axenically** *adj.*

axenize *or* **axenise** to render axenic.

axenite an organism grown axenically.

axial **1** of, relating to, or being an **axis** (def. 1 or 2); located on or close to such an axis. **2** *(in stereochemistry) Symbol*: a. *See* **conformation**.

axial ratio the ratio of the length of the major axis to that of the minor axis of a prolate ellipsoid of rotation, a model often used for a protein or other macromolecule in solution.

axis **1** a straight line about which a body or three-dimensional figure, e.g. a crystal, is considered to rotate. **2** one of the reference lines of a co-ordinate system. **3** the second vertebra of the neck in higher vertebrates.

axis of rotation *see* **rotation axis**.

axis of symmetry *see* **symmetry, axis of**.

axokinin a heat-stable phosphoprotein, M_r 56 000, present in flagella and cilia of vertebrate and invertebrate species. Its cyclic AMP-dependent phosphorylation is required for initiation and maintenance of flagellar motility.

axon the long process of a neuron that conducts nerve impulses, usually away from the cell body to the terminals which are the site of storage and release of neurotransmitter. *Compare* **dendrite**.

axonal transport the directed transport of organelles and molecules along the axon of a neuron. It can be anterograde (i.e. outwards from the cell body) or retrograde (i.e. towards the cell body).

axoneme the bundle of microtubules and associated proteins that forms the core of cilia and flagella in eukaryotic cells and is responsible for their movements.

axoplasm the cytoplasm of the axon of a neuron, especially after it has been extruded from the axon.

aza- *prefix* **1** *(in systematic chemical nomenclature)* denoting the replacement of a designated carbon atom (together with one associated hydrogen atom) by a nitrogen atom. **2** *(in trivial chemical names)* denoting presence of one or more nitrogen atoms.

azaserine *trivial name for* serine diazoacetate; *O*-diazoacetyl-L-serine, N_2=CH–CO–O–CH_2–CH(NH_2)–COOH; an antibiotic substance produced by *Streptomyces* spp. It is an inhibitor of amidotransferase enzymes and interferes with purine synthesis; it also retards the growth of transplantable animal neoplasms and is a specific inhibitor of L-glutamate ferredoxin oxidoreductase (transaminating), EC 1.4.7.1, in ammonium assimilation in plants.

azathioprine 6(1-methyl-4-nitro-5-imidazolyl) mercaptopurine: 6-[(1-methyl-4-nitroimidazol-5-yl)thio]purine; a derivative of **mercaptopurine**, into which it is converted *in vivo*. It is useful as an immunosuppressive and antimitotic agent. *One proprietary name*: Imuran.

azelaic acid 1,7-heptanedicarboxylic acid, nonanedioic acid; a substance that acts as a substitute for biotin in the growth of a number of microorganisms and is proposed as an intermediate in biotin biosynthesis from oleic acid.

azeotrope a mixture of two or more liquids that distils without change in composition and has a constant boiling temperature.

azide **1** any organic compound containing the monovalent azido group, –N=N^+=N^-. **2** the ion N_3^-, derived from hydrazoic acid, HN_3. This ion blocks the electron transport chain by reacting with the ferric form of cytochrome aa_3 and thus acts as an inhibitor of respiration. **3** any salt or ester of hydrazoic acid.

azidothymidine *see* **AZT**.

azo the bivalent group –N=N–. It participates in noncyclic covalent linkage in organic molecules forming **azo compounds** or **diazo compounds**.

azocoll an insoluble bright-red collagen-rich proteinaceous material prepared by dyeing powdered cowhide or kangaroo-tail tendon with a dye prepared from tetrazolized benzidine, disodium 2-naphthol-3,6-disulfonate and sodium acetate. It is digested by most types of proteinase, the consequent solubilization of dye forming the basis of a simple nonspecific technique for the assay of proteolytic activity.

azo compound any organic compound with the general formula R–N=N–R′. Such compounds thus contain the bivalent azo group in covalent linkage, each nitrogen atom being linked to a carbon atom and replacing one hydrogen atom of each of the parent molecules RH and R′H. The latter may be the same or different, aliphatic or aromatic; e.g. azomethane, CH_3–N=N–CH_3; naphthalene-2-azobenzene, $C_{10}H_7$–N=N–C_6H_5. *Compare* **diazo compound**.

azoferredoxin *or* **protein II** a very oxygen-sensitive iron–sulfur protein that is a component of the **nitrogenase** enzyme system. It is a dimer of identical ≈30 kDa peptide chains. Each dimer contains two iron atoms, four S^{2-} groups, and 12 titratable thiol groups. In nitrogenase it is believed to be the electron carrier responsible for the reduction of molybdenum in **molybdoferredoxin**.

azomethine strictly, any **imine** having the more limited general structure RR′C=NR where R and R′ are any organyl groups, but often extended to include any compound where R′ is H, the term then being considered to be synonymous with **Schiff base**.

azoprotein any of the modified proteins formed by coupling an aromatic diazo compound to one or more of the tyrosine residues of a protein, e.g. azoalbumin, azocasein.

azotemia *former term for* the accumulation of abnormally large concentrations of nitrogenous compounds, especially urea, in the blood.

Azotobacter a genus of Gram-negative strictly aerobic soil bacteria, all members of which can effect **nitrogen fixation**.

azotoflavin a somewhat larger than normal **flavodoxin** that is believed to act as a one-electron carrier between ferredoxin and azoferredoxin during nitrogen fixation in some bacteria, e.g. *Azotobacter*.

AZT *abbr. for* azidothymidine; 3′-azido-3′-deoxythymidine; *other names*: zidovudine; Retrovir; an analogue of thymidine, the phosphorylated form of which is an inhibitor of **reverse transcriptase** in **retroviruses**; it also terminates DNA synthesis. AZT undergoes phosphorylation in human T-cells to a nucleoside 5′-triphosphate, which competes with thymidine triphosphate and serves as a chain terminating inhibitor of HIV reverse transcriptase. It is used clinically to treat patients with **HIV** infection and **AIDS**.

azurin any member of a group of brilliant blue copper-containing proteins of low M_r found in some bacteria and thought to transfer electrons to cytochrome oxidase. Example from *Pseudomonas fluorescens* biotype B: database code AZUR_PSEFB, 128 amino acids (13.78 kDa).

azurophil(e) *or* **azurophilic** staining readily with blue aniline dyes.

azurophil(e) granule *or* **primary granule** a blue-staining lysosome of neutrophil leukocytes.

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Bb

b *symbol for* **1** molality. **2** one of two van der Waals coefficients. **3** breadth.

B *symbol for* **1** boron. **2** a residue of either of the α-amino acids L-aspartic acid or L-asparagine when the state of amidation is uncertain (alternative to Asx). **3** a residue of an incompletely specified base in a nucleic acid sequence that may be cytosine or guanine or either thymine (in DNA) or uracil (in RNA). **4** the ribonucleoside (5-)bromouridine (alternative to BrUrd). **5** the B blood group. *See* **ABO system**.

B *symbol for* **1** Napierian absorbance (*see* **absorbance**). **2** magnetic flux density (bold italic).

-*B* conformational descriptor designating the boat conformation of a six-membered ring form of a monosaccharide or monosaccharide derivative. Locants of ring atoms that lie on the side of the structure's reference plane from which the numbering appears clockwise are indicated by superscripts preceding the letter, and those that lie on the other side of the reference plane by subscripts following the letter; e.g. methyl 2,6-anhydro-α-D-altropyranoside-$^{2,5}B$. *See also* **conformation** (under *cyclic compounds*).

***B*$_{max}$** *symbol for* the amount of drug required to saturate a specific population of receptors in a membrane sample and hence an index of the density of receptor binding sites in the sample. It is usually derived from Scatchard analysis (*see* **Scatchard plot**) or from nonlinear regression analysis of data from a saturation binding assay.

Ba *symbol for* barium.

Baa helices *abbr. for* basic amphiphilic α helices; α helices that contain an array of basic amino-acid residues (His, Lys, or Arg) on one side and hydropathic residues on the other. They are found, e.g., in the calmodulin-binding regions of many proteins.

Babes–Ernst body *or* **Babes–Ernst granule** a **volutin granule** seen in *Corynebacterium diphtheriae*. [After Victor Babes (1854–1926), Romanian bacteriologist, and Paul Ernst (1859–1937), German pathologist.]

BAC *abbr. for* bacterial artificial chromosome, based on the F factor (**F plasmid**) of *Escherichia coli*. *Compare* **YAC**.

Bacillaceae a family of eubacteria that includes the genera *Bacillus* and *Clostridium*.

bacillary *or* **bacillar** **1** of, relating to, caused by, or containing bacilli. **2** *an alternative term for* **bacilliform** (def. 1).

bacilliform **1** rod-shaped. **2** resembling a bacillus.

bacillus (*pl.* **bacilli**) any straight rod-shaped bacterial cell.

Bacillus a genus of large rod-shaped Gram-positive eubacteria belonging to the family Bacillaceae. Its members are aerobic or facultatively anaerobic, spore-bearing organisms. *B. subtilis* has become widely established as a vehicle for genetic engineering and many cloning **vectors** are available. *B. thuringiensis* synthesizes a toxin that is active against insects; different strains of the bacterium produce different forms of the toxin specific for different insect species.

bacitracin a cyclic antibiotic polypeptide complex produced by *Bacillus subtilis* and *B. licheniformis*. Commercial bacitracin is a mixture of at least nine bacitracins, mostly bacitracin A. Bacitracin A contains, in addition to several L amino acids, a number of D amino acids. Bacitracin inhibits bacterial cell wall synthesis by blocking the dephosphorylation of undecaprenyl diphosphate (undecaprenyl pyrophosphate) to the monophosphate form; it similarly inhibits the dephosphorylation of dolichyl diphosphate thereby blocking the formation of the core oligosaccharides of glycoproteins.

backbone **1** *(in biochemistry)* the sequence of bonded atoms of a polymer to which the side groups and/or the side chains are attached. **2** *(in zoology)* the vertebral column or spine.

backcross **1** any cross of a first-generation hybrid, F_1, with one parent or an individual genetically identical to one of the two parents. **2** the offspring of such a mating.

back-flush *an alternative term for* **back-wash**.

background any intrusive sound or electronic signal registered by a detector but not coming from the source being measured, e.g. the radioactivity registered by a counter in the absence of a radioactive sample.

back mutation *an alternative term for* **reverse mutation**.

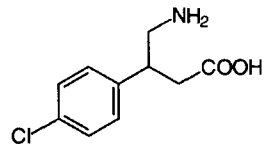
back scattering *an alternative term for* **backward scattering**.

back titration an indirect titration procedure in which a measured excess of the reagent is added and the amount remaining after reaction with the analyte is titrated back to an end-point, the proportion consumed in the reaction being obtained by difference.

backward scattering *or* **back scattering** any scattering of radiation in a direction towards the source of the incident radiation.

back-wash *or* **back-flush** to pass a fluid through a chromatographic column in the direction opposite to that of the eluent flow. It is useful, e.g., to relieve bed-compression and to remove entrained gas.

baclofen γ-amino-β-(*p*-chlorophenyl)butyric acid; 3-(aminomethyl)-3-(4-chlorophenyl)propanoic acid; a 4-chlorophenyl derivative of γ-aminobutyric acid (GABA) that acts as a selective agonist for the **$GABA_B$ receptor** and inhibits the release of other neurotransmitters in the central nervous system. It is used for its antispastic (muscle-relaxing) effects.



bactenecin any of several highly cationic polypeptides, originally isolated from bovine neutrophil granules but also found in sheep, that exert, *in vitro*, a potent antimicrobial activity, possibly due to inhibition of respiratory chain function. Example, bactenecin 5 (precursor) from *Bos taurus*: database code BCT5_BOVIN, 176 amino acids (20.03 kDa); residues 131–173 are bactenecin 5.

bacteremia *or (esp. Brit.)* **bacteraemia** the presence of live bacteria in the blood.

bacteria *plural of* **bacterium**.

Bacteria one of three superkingdoms (domains) of cellular organisms, the others being Archaea and Eukarya. Bacteria are unicellular and anucleate i.e. **prokaryotes**. They embrace a great diversity of forms, major divisions including the Cyanobacteria, Proteobacteria (which includes Gram-negative bacteria), and Gram-positive bacteria.

bacterial conjugation the process whereby genetic material is transferred from one bacterial cell (the donor) to another (the recipient). Material is usually transferred via a tubelike pilus, which extends from the donor cell to the recipient cell. The terms 'donor' and 'recipient' are preferred to 'male' and 'female' since the latter refer only to the presence or absence of **F plasmid**.

bacterial histone *see* **H-NS**.

bacterial photosynthetic reaction centre *see* **photosynthetic reaction centre**.

bacterial porin *see* **porin**.

bacterial recombinant *see* **transconjugant**.

bacterial virus *see* **bacteriophage**.

bactericide *or* **bacteriocide** any agent (biological, chemical, or

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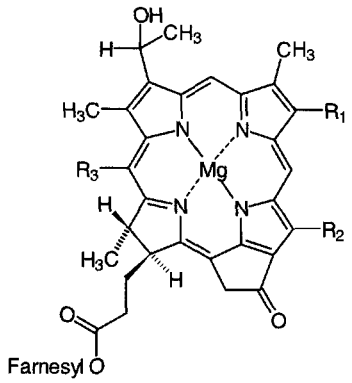
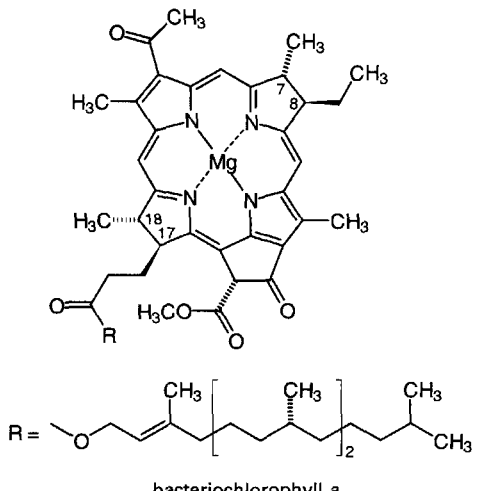
physical) that destroys bacteria. —**bactericidal** *or* **bacteriocidal** *adj.*

bactericidin *or* **bacteriocidin** *or* **bacteriolysin** any antibody that, with **complement**, kills bacteria against which it is active.

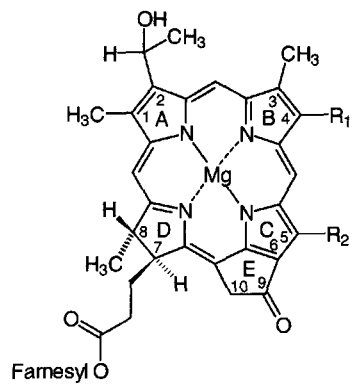
bacteriochlorophyll any of the **chlorophylls** of photosynthetic bacteria. They differ structurally from the chlorophylls of higher plants. Bacteriochlorophylls *a* to *g* are known. Bacteriochlorophylls *a* and *b* are the best known, being the photosynthetic pigments of purple bacteria. Their purple colour results from the fact that they are reduced in both rings B and D, and thus may be regarded as tetrahydropyrroles. Tetrapyrrole carbon atoms and carbon rings are numbered according to the Fischer and IUPAC systems as indicated below. The structure of bacteriochlorophyll *a* is shown. Bacteriochlorophyll *b* has $=CH-CH_3$ in place of the ethyl group on ring B of bacteriochlorophyll *a*. In some bacteriochlorophylls *a* the phytyl group may be replaced by a geranylgeranyl group. Bacteriochlorophylls *c*, *d*, and *e* are antenna pigments of Chlorobiaceae, located in chlorobium vesicles (a core structure is shown). These are dihydropyrrole structures, being reduced in ring D only. The esterifying alcohol is farnesol. In these bacteriochlorophylls, the side chain R_1 (see core structure) on ring B varies, being ethyl, *n*-propyl, or isobutyl (in bacteriochlorophyll *d* neopentyl is also possible). On ring C the side chain R_2 is ethyl (in bacteriochlorophyll *d* methyl is also possible). R_3 is methyl in bacteriochlorophylls *c* and *e*, and H in bacteriochlorophyll *d*.



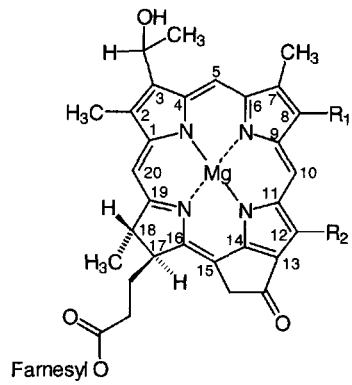
bacteriochlorophyll *c, d, e* core structure



bacteriochlorophyll *a*



tetrapyrrole carbon numbering Fischer system



tetrapyrrole carbon numbering IUPAC system

bacteriocide *a variant spelling of* **bactericide**.

bacteriocidin *a variant spelling of* **bactericidin**.

bacteriocin any of a heterogeneous group of polypeptide antibiotics that are secreted by certain bacterial strains and are able to kill cells of other susceptible (frequently related) strains after adsorption at specific receptors on the cell surface. They include the colicins, and their mechanisms of action vary. Examples: colicin E1 from *Escherichia coli*: database code CEA1_ECOLI, 522 amino acids (57.21 kDa); this is a channel-forming transmembrane protein that results in membrane depolarization; colicin E3 from *E. coli*: database code CEA3_ECOLI, 541 amino acids (57.90 kDa); this is an rRNA ribonuclease; plantaricin A from *Lactobacillus plantarum*: database code (of precursor) PLNA_LACPL; plantaricin A is a channel-forming peptide dimer of α and β chains; the amino-acid sequence of the β chain is:

AYSLQMGATAIKQVKKLFKKWGW;

the α chain lacks the N-terminal A. —**bacteriocinogenic** *adj.*

bacteriocinogenic factor any **plasmid** that carries genetic information for the production of a **bacteriocin**. Generally only a small proportion of cells containing the factor actually produce bacteriocin. *See also* **Col plasmid**.

bacterioferritin a bacterial b_1-type **cytochrome** of 18 kDa subunit containing 13–20% w/w of iron. It has similar properties to mammalian **ferritin**. It may be concerned with iron or/and electron storage in the bacterium. Similar proteins may be present in other species of bacteria. Example from *Azotobacter*

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vinelandii: database code BFR_ECOLI, 158 amino acids (18.49 kDa). These proteins are oligomers of 24 identical subunits.

bacteriology the branch of science that deals with the study of **bacteria**.

bacteriolysin *an alternative term for* **bactericidin**.

bacteriolysis the lysis of bacteria. —**bacteriolytic** *adj.*

bacteriophaeophytin *a variant spelling of* **bacteriopheophytin**.

bacteriophage *or* **phage** *or* **bacterial virus** any virus that can infect and multiply in a bacterium. Phages parasitize almost every group of prokaryotes. Commonly they consist of a core of nucleic acid enclosed within a protein coat, the capsid; additional components, e.g. lipid, occur in some phages. Depending on the type of phage, the nucleic acid may be either DNA (single-stranded or double-stranded) or RNA (single-stranded), and may be either linear or circular. Phages may be filamentous, polyhedral, or polyhedral and tailed; the tubular tails, to which one or more tubular tail fibres are attached in certain circumstances, are involved in attachment of the phages to the bacterial surface and for the injection of the DNA into the host cells. The smallest phages, e.g. ϕX174, are ≈25 nm in diameter, whereas tailed polyhedral phages, such as the **T-even phages**, are 200–250 nm long, while filamentous phages measure roughly 800 nm × 5 nm. In general, a given bacteriophage can infect only one particular species, or strain, or group of closely related strains, though a given strain may be susceptible to infection by a number of different phages. Bacteriophages can bring about **transduction** (def. 1) between bacterial cells. *Compare* **cyanophage**. *See also* **(bacterio)phage conversion**, **lysogeny**, **phage induction**, **phage typing**, **prophage**, **temperate phage**, **virulent phage**.

(bacterio)phage conversion *or* **prophage-mediated conversion** *or* **lysogenic conversion** the introduction of new properties to a host bacterium by the genome of an infecting lysogenic prophage. Such properties may include resistance to lysis by related phages, changes in antigenic constitution, or the appearance of toxigenicity.

bacteriophage vector *see* **cloning vector**.

bacteriopheophytin *or (esp. Brit.)* **bacteriophaeophytin** a **bacteriochlorophyll** in which Mg^{2+} is replaced by 2 H^+.

bacteriorhodopsin a retinal-containing protein, resembling animal **rhodopsin**, formed by *Halobacterium halobium* and other halophilic Archaea and inserted into patches of **purple membrane** in the cell surface. The purple membranes serve as light-operated **hydrogen-ion pumps** to translocate hydrons from the inside to the outside of the cells. Example from *H. halobium* (precursor): database code BACR_HALHA, 262 amino acids (28.22 kDa); residues 1–13 form the propeptide and the C-terminal Asp is also missing from the mature protein, which is a seven-helix transmembrane protein of known 3-D structure and a model for **opsin** and related G-protein-linked receptors in eukaryotic cells.

bacteriostatic *or* **bacteristatic** describing a drug, antibiotic, or other agent that inhibits the growth and multiplication of bacteria. *Compare* **bactericide**. —**bacteriostasis** *n.*

bacterium (*pl.* **bacteria**) any of a vast and ubiquitous group of prokaryotic microorganisms that exist as single cells or in clusters or aggregates of single cells. Most authorities now place them in the exclusively prokaryotic kingdom Monera, along with the **cyanobacteria** (blue-green algae). The majority of bacteria possess a rigid cell wall; those lacking this feature are termed **Archaea**. Bacteria, Archaea, and Eukarya constitute the three primary Kingdoms (domains). —**bacterial** *adj.*

Bacteroides a genus of Gram-negative anaerobic rodlike bacteria. Mostly nonmotile, they are commonly present in the alimentary and urogenital tracts of mammals and may behave as opportunistic pathogens.

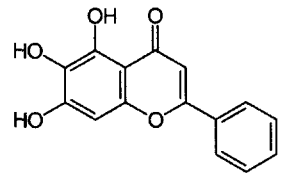
bactoprenol *an alternative name for* **undecaprenol**.

Bactrim *see* **sulfamethoxazole**.

baculovirus any of a group of DNA viruses that are known to multiply only in invertebrates and are now classified in the family Baculoviridae. Their genome consists of double-stranded circular DNA of 58–100 MDa. Because of their host range they have potential as pest-control agents. Baculovirus vectors are valuable as a means of expressing certain animal proteins (*see* **expression system**).

BAF *abbr. for* B-cell activating factor (*see* **interleukin 1**).

baicalein 5,6,7-trihydroxyflavone; a pigment (greenish-brown in dilute alkali) found in the root of *Scutellaria baicalensis*. It is a selective 12-lipoxygenase inhibitor. Baicalein inhibits leukotriene biosynthesis and cellular Ca^{2+} uptake and mobilization.



bait a hybrid protein containing the GAL4 DNA-binding domain, used in the **yeast two-hybrid system**. *See also* **bait region**.

bait region a restricted region in the sequence of **α_2-macroglobulin** (α_2M) that is cleaved by proteinases in the process leading to the conformational changes instrumental in the proteinase inhibitory function of α_2M. The bait region occurs in all α-macroglobulins but shows great variation in length and amino-acid sequence between different α-macroglobulin and animal species. In human α_2M, it covers approximately residues 666–706. Outside of the bait region, α_2M from different species shows very high sequence homology. *See also* **trap hypothesis**.

bakers' yeast any of various strains of the yeast *Saccharomyces cerevisiae* that are used in baking.

baking soda *see* **soda**.

BAL *abbr. for* British anti-lewisite (*see* **dimercaprol**).

balance **1** *(in physiology)* the relation between the intake of a particular nutrient and its excretion (or the excretion of its metabolites). **2** any instrument for determining the equality in mass of two objects (or sets of objects). In cases where one (set) is of known mass the mass of the second (set) is thus obtained; e.g. an analytical balance. **3** any instrument designed to measure the weight of an object, e.g. spring balance, torsion balance.

balanced growth a type of growth such that over a time interval (within the exponential phase) every extensive property of the growing system increases by the same factor. Balanced growth for an individual cell requires that each cell after division is an exact replica of the one of the previous cycle.

balanced salt solution any solution designed to provide a normal environment, in terms of ionic composition, pH, and osmotic pressure, for cells in tissue culture.

balance study any study to determine **balance** (def. 1).

balata *see* **rubber**.

BALB/c a strain of inbred white mice that readily develop experimental myelomatosis.

Balbiani ring a large **puff** of giant chromosomes present during a greater portion of larval development in members of the Diptera. The structural modification of specific loci is characteristically large and ring-shaped. [After Eduard Gérard Balbiani (1823–99), French entomologist who reported it in 1881.]

Baltimore, David (1938–), US microbiologist and molecular biologist distinguished for his studies of viral nucleic-acid biosynthesis, particularly his discovery (at the same time as H. M. Temin) of reverse transcription by the enzyme RNA-directed DNA polymerase in the virions of tumour-producing retroviruses, and for the classification of animal viruses named after him; Nobel Laureate in Physiology or Medicine

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(1975) jointly with R. Dulbecco and H. M. Temin 'for their discoveries concerning the interaction between tumour viruses and the genetic material of the cell'.

Baltimore classification a method of classification of animal viruses based on the nature of the genome and the mechanism for synthesis of mRNA, which is always regarded as the **plus strand** (def. 2). There are six classes:

Class I Viruses having a double-stranded (ds) DNA genome that make mRNA by asymmetric transcription. In many, different mRNA species come from different DNA strands.

Class II Viruses having a single-stranded (ss) DNA genome of the same polarity as the mRNA. Some have strands of both polarity in different particles.

Class III Viruses having a dsRNA genome that make mRNA by asymmetric transcription. Most have multiple pieces of dsRNA, each of which apparently contains the information for the synthesis of a single protein.

Class IV Viruses having an ssRNA genome that make mRNA of base sequence identical to the genomic RNA.

Class V Viruses having an ssRNA genome that make mRNA with a base sequence complementary to the genomic RNA.

Class VI **Retroviruses** having an ssRNA genome and a DNA intermediate in their growth.

band **1** an **absorption band** in an electromagnetic spectrum. **2** a zone of (macro)molecules such as that obtained in density-gradient centrifugation, zone electrophoresis, isoelectric focusing, chromatography, or other similar method. **3** any of the zones readily distinguishable by microscopy in a **sarcomere** of a muscle. **4** the specific association of a large number of **chromomeres** at the same level in somatically paired **polytenic** giant chromosomes of members of the Diptera. *See also* **cytochrome absorption bands**.

band centrifugation *see* **isopycnic centrifugation**.

band compression inadequate separation of the bands on a gel electrophoretogram, especially in DNA sequencing gels. It results in poor resolution and difficulties in interpretation.

band electrophoresis *an alternative name for* **zone electrophoresis**.

banding the formation of distinct bands or zones in density-gradient centrifugation, column chromatography, or other separation techniques.

banding density the density of the suspending medium at which a particular type of particle, e.g. a cell organelle, forms a band during centrifugation in a specified density gradient.

band intensity *(in NMR spectrometry)* the area under the band between the signal trace and the baseline. *See* **nuclear magnetic resonance**.

band-pass filter **1** an electric circuit or other device that transmits only frequencies within a selected band. **2** an **interference filter**.

band protein erythrocyte proteins are referred to as bands, numbered according to the position they occupy on electrophoresis gels. Some of the more important bands are: 1 and 2, α and β **spectrin**; 3, an anion channel protein; 4.1, always referred to as such, is involved in spectrin junctions; 5, **actin**.

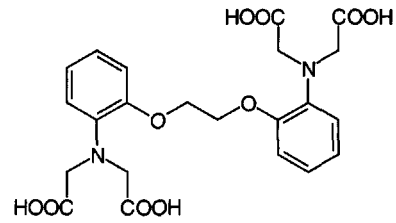
band width *(in NMR spectrometry)* the distance between the sides of the band at half the band height of a reasonably smooth and symmetrical band. *See* **nuclear magnetic resonance**.

Bangasome *or* **Bangosome** *(colloquially) an alternative name for* **liposome**. [After its inventor, Alec Douglas Bangham (1921–), British biophysicist and medical scientist.]

Banting, (Sir) Frederick Grant (1891–1941), Canadian surgeon, physiologist, and endocrinologist distinguished for his discovery (with C. H. Best) of a means of extracting the hormone insulin from pancreatic tissue and for demonstrating its anti-diabetic efficacy; Nobel Laureate in Physiology or Medicine (1923) jointly with J. J. R. Macleod 'for the discovery of insulin'. *See also* **Best, Macleod**.

Bantu siderosis *see* **iron overload**.

BAPTA 1,2-bis(*o*-aminophenoxy)ethane-*N*,*N*,*N*′,*N*′-tetraacetate; a Ca^{2+} chelator exhibiting a 10^5-fold greater affinity (110 nM) than for Mg^{2+}. Its UV absorption maximum is at 254 nm which, after Ca^{2+} is bound, shifts to 279 nm, a property that can be exploited in its use as an indicator of intracellular Ca^{2+} concentration. Its esterified form can enter cells where it is hydrolysed to BAPTA.



bar a unit of pressure temporarily approved for use with SI units. 1 bar = 10^5 Pa = 10^5 N m^{-2}.

barbed end *see* **plus end**.

barbital *or* **barbitone** 5,5-diethylbarbituric acid; 5-diethylmalonylurea; 5,5-diethyl-2,4,6(1*H*,3*H*,5*H*)-pyrimidinetrione; a long-acting depressant of the central nervous system, widely used as a buffer substance; pK_a = 7.98 (25 °C), 8.06 (20 °C). *One proprietary name*: Veronal.

barbiturate **1** the tautomeric anion derived from barbituric acid (malonylurea; 2,4,6(1*H*,3*H*,5*H*)-pyrimidinetrione). **2** any mixture of free barbituric acid and its anion. **3** any salt of barbituric acid. **4** any of various pharmacologically active derivatives of barbituric acid, including barbitone, pentobarbitone, phenobarbitone, and thiopentone. Barbiturates are potent CNS depressants that potentiate the actions of GABA by binding to the $GABA_A$ receptor. Pentobarbitone and thiopentone are used to induce anesthesia.

Barcroft apparatus *or* **Barcroft respirometer** a differential respirometer for studying gas exchange of cells, tissue slices, or tissue homogenates, now rarely used. It is a closed system comprising two flasks of equal volume connected by a U-shaped manometer (the Barcroft manometer). In operation, both flasks contain the same volumes of liquid and gas; one, the reaction flask, contains the cells or tissue; the other, the compensation flask, is free from cells or tissue and serves to compensate for changes in temperature and barometric pressure during the course of an experiment. The respirometers are arranged so that they may be shaken with the flasks in a constant-temperature bath. The reading of the apparatus is the difference between the levels of the manometer fluid in the two sides of the manometer. [After Joseph Barcroft (1872–1947), British physiologist, who described it in 1908.]

Barfoed's reagent a solution containing cupric acetate in dilute acetic acid that is reduced when heated with monosaccharides but not with disaccharides or oligosaccharides. [After Christen Thomsen Barfoed (1815–99), Swedish physician.]

barn *symbol*: b; a non-SI unit of area equal to 10^{-28} m^2. It is used as a unit of atomic nuclear cross section.

barnase *or* **ribonuclease BA**; a small extracellular endoribonuclease from *Bacillus amyloliquefaciens*. Its action involves formation of a 2′:3′-cyclic phosphate (*see* **ribonuclease**). It has been studied as a model for protein folding. The sequence and 3-D structure are known: database code RNBR_BACAM, 157 amino acids (17.47 kDa).

baroceptor *a variant spelling of* **baroreceptor**.

barometer an instrument for measuring the pressure of the atmosphere.

barometric pressure the pressure exerted by the atmosphere at a given place and time. It is often expressed in terms of the supported height of a column of mercury, usually measured in millimetres. The SI unit is the **pascal**. Other non-SI units frequently used in addition to the **millimetre of mercury** are the **atmosphere**, the **bar**, and the **torr**.

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baroreceptor *or* **baroceptor** any physiological receptor that is sensitive to changes in pressure, especially the sensory nerve endings in the carotid sinus that set off nerve impulses in response to alterations in blood pressure at that point.

Barr body *see* **sex chromatin**.

barrier an extracellular protein, probably a proteinase, excreted by yeast cells of mating type **a**. Its role may be to act as an antagonist of the α-type mating pheromone and establish optimal pheromone concentration for conjugation. Example (precursor) from *Saccharomyces cerevisiae*: database code BAR1_YEAST, 587 amino acids (63.66 kDa).

Barton, (Sir) Derek Harold Richard (1918–98), British organic chemist; Nobel Laureate in Chemistry (1969), the prize being shared with O. Hassel 'for their contributions to the development of the concept of conformation and its application in chemistry'.

barwin a barley seed protein (possibly a lectin) involved in defence mechanisms. It is closely related to the C-terminal domain of proteins encoded by wound-induced plant genes. It gives its name to a family of such proteins. Example, database code BARW_HORVU, 125 amino acids (13.77 kDa); 3-D structure known.

basal **1** at, of, or being a **base** (def. 4). **2** at, of, or being the minimum level for maintaining the normal or essential functioning of an organism.

basal body **1** *(in prokaryotes)* a structure that apparently attaches the **flagellum** (def. 1) to the cell envelope. The proximal end of the flagellum, the hook, appears curved and thickened and leads into the basal body, which consists of parallel ring-shaped structures, arranged around a rod-shaped core. The rings of the basal body make contact with the layers of the cell envelope. **2** *(in eukaryotes)* a structure at the base of a cilium consisting of spherical granules or short rods arranged in rows below the cell surface. Electron microscopically they are cylindrical bodies, 300–500 nm long and 120–150 nm in diameter, open at one or both ends. They consist of nine sets of triplet microtubules, each triplet containing one complete microtubule fused to two incomplete microtubules.

basal granule *an alternative term for* **basal body** (esp. in ciliated epithelium).

basal lamina a thin sheet of proteoglycans and glycoproteins, especially **laminin**, secreted by cells as an extracellular matrix, forming a region between the cells and adjacent connective tissue. The basal lamina has important functions in the organization of tissues including an influence on cell polarity, cell differentiation, and cell migration. The basal lamina is subdivided into the ***lamina lucida*** (an electron-lucent region) immediately adjacent to the cell layer, and the ***lamina densa*** (an electron-dense region) external to it. Frequently there is a further outermost layer, the ***lamina reticularis***, containing collagen fibrils. The three laminae are often collectively referred to as the **basement membrane**.

basal medium any culture medium that will support the growth of nutritionally undemanding chemoorganotrophs.

basal metabolic rate *abbr.*: BMR; the rate of energy metabolism of an animal at rest but not asleep. It is measured with the animal in a 'comfortable' ambient temperature, and in the postabsorptive state, at least 12 hours after taking food. It may be determined from the oxygen consumption and carbon dioxide (and urinary nitrogen) excretion, or from the heat production of the animal.

base **1** *(in chemistry)* **a** a **Brønsted–Lowry base**. **b** a **Lewis base**. *See also* **acid** (def. 2). **2** *(in molecular biology)* any purine or pyrimidine that occurs as a component residue in polynucleotides or nucleic acids. Purines and pyrimidines are **nitrogen bases**, hence the terminology. **3** a unit of length of a polynucleotide or nucleic acid, equal to one nucleotide residue. Large molecules are usually measured in kilobases (10^3 bases; *symbol*: kb) or megabases (10^6 bases; *symbol*: Mb). *See also* **nitrogenous base**. **4** *(in mathematics)* **a** the number of units in a system of counting that is equivalent to one unit in the next higher counting place. **b** the number that when raised to a specified power, its **exponent**, has a logarithm equal to the specified power. **5** the bottom or supporting part of anything; the point of attachment of an organ or part to an organism.

base analogue *or (esp. US)* **base analog** any unnatural purine or pyrimidine base that can be incorporated *in vivo* into DNA but that, because of its different properties, causes altered base-pairing during incorporation or in subsequent DNA replication. Thus 5-bromouracil, an analogue of thymine, pairs with guanine thereby causing transitions of A–T → G–C. Similarly, 2-aminopurine, an analogue of adenine, pairs with cytosine thereby causing transitions of A–T → G–C. Some base analogues have been used as anticancer and antivirus agents.

base calling the automated reading of DNA-sequencing gels using a scanner and appropriate software.

base composition the relative amounts of the various purines and pyrimidines occurring in a specimen of polynucleotide or nucleic acid. It is often expressed as moles percent.

baseline an imaginary line or a standard or reference value, etc. by means of which measurements may be compared, especially the zero line in the tracing of a chromatogram, spectrum, ultracentrifuge pattern, etc.

basement membrane a thin layer of dense material found in various animal tissues interposed between the cells and adjacent connective tissue. It consists of the **basal lamina**, comprising fine fibrillar material in a glycoprotein matrix, plus an associated layer of reticulin fibres. Occurring in, e.g., capillary linings, kidney tubules, lung alveoli, and renal glomeruli, basement membrane has a supportive function in some tissues and may also act as a passive selective filter for substances diffusing in or out of the cells; e.g. in renal glomeruli it retains protein molecules. It gives a strong periodic acid–Schiff reaction.

base pair *symbol*: bp; any of the possible pairings between two bases in opposing strands of double-stranded DNA or RNA molecules. Adenine forms a base pair with thymine (in DNA) or uracil (in RNA) and guanine with cytosine, hence the number of adenine residues equals the number of thymine (and/or uracil) residues while the number of guanine residues equals that of the cytosine residues. *See also* **Chargaff's rules**. —**base-pair** *vb.*; **base-pairing** *n.*

base-pair ratio *see* **Chargaff's rules**.

base sequence the sequential order of nucleotide residues in a polynucleotide or nucleic acid molecule.

base stacking the arrangement of base pairs in parallel planes, at an angle to the helix axis, in the interior of a helical double-stranded polynucleotide or nucleic acid molecule.

base triplet any sequence of three bases in a nucleic acid that codes for an amino acid, or some other signal, in protein synthesis. *Compare* **anticodon**; **codon**.

basic **1** of, relating to, containing, or characteristic of a **base** (def. 1). *Compare* **acidic** (def. 1). **2** having an alkaline reaction; of or relating to an aqueous solution having a pH value >7.0. *Compare* **acidic** (def. 2).

basic amino acid any amino acid possessing a net positive charge at neutral pH.

basic azo-dye binding protein *abbr.*: B-ABP; a 45 kDa (Sephadex) protein, isolated from the soluble cell supernatant fraction from livers of rats given 4-dimethylaminoazobenzene. It was later named **ligandin**.

basic dissociation constant *or* **basicity constant** *symbol*: K_b; the thermodynamic dissociation constant for the dissociation of a **base** (def. 1, 2). For a dilute solution of a weak base, B, dissociating in water according to the equilibrium:

$$BOH \rightleftharpoons B^+ + OH^-,\ K_b = a_{B^+} \times a_{OH^-} / a_{BOH}$$

where a is the **activity** of the species designated by the subscripts. The activity of the water has been omitted from the equation since it may be taken as unity in dilute aqueous solution. K_b is a measure of the strength of a base, i.e. of its ability to accept hydrons from water (*compare* **acid dissociation con-**

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stant; *see also* **pK**). The concept is no longer used since the conjugate acid, B^+, may be considered as an acid and an acid dissociation constant, K_a, for it defined. Also, in aqueous solutions

$$K_a \times K_b = [H^+][OH^-] = K_w,$$

where K_w is the ion product of water, whence K_b may be calculated from K_a or vice versa.

basic dye *or* **basic stain** any cationic dye that binds to, and hence stains, anionic macromolecules or other materials.

basic salt any salt containing hydroxyl or oxide groups in partial replacement of, or in addition to, ions or groups derived from an acid, e.g. basic lead acetate, $(CH_3COO)_2Pb{\cdot}Pb(OH)_2$.

basic stain *an alternative term for* **basic dye**.

basic zipper *see* **bZIP**.

basolateral surface the surface of an epithelial cell that adjoins underlying tissue. *Compare* **apical surface**.

basonuclin a **zinc finger** nuclear protein of epidermis, likely to be a transcription factor specific for squamous epithelium and its keratinocytes prior to terminal differentiation. It is present mainly in the nuclei of the basal cell layer. Example from human: database code BASO_HUMAN, 993 amino acids (110.85 kDa).

basophil *or* **basophil(ic) leukocyte** a polymorphonuclear phagocytic leucocyte of the myeloid series that is distinguished by the presence of coarse cytoplasmic granules that stain with basic dyes. The granules are believed to contain histamine, heparin, and other vasoactive amines. Basophils are closely related to **mast cells** and constitute <0.5% of blood leukocytes.

basophilia **1** the property of being **basophilic**. **2** an increase in the number of **basophils** circulating in the blood.

basophilic staining readily with basic dyes.

basotropic seeking a basic environment; a term used especially in connection with protein kinases that have a requirement for basic residues near the target residue. *Compare* **acidotropic**.

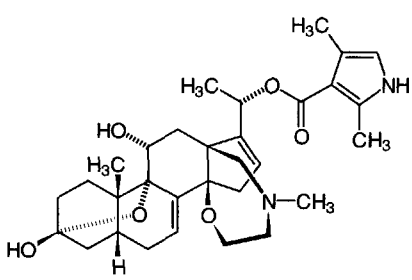
batch a quantity of material produced or processed in one operation on a single occasion, as opposed to a continuous operation; hence batch adsorption, batch culture, etc.

batch elution a method of column chromatography in which conditions are chosen to ensure complete retention of the material under investigation, using the minimal amount of stationary phase, followed by elution with a solvent or buffer that ensures complete and rapid removal in the minimal possible volume.

batch process *(in biotechnology)* a process in which a bioreactor is loaded with substrates inoculated with microorganisms or enzymes and allowed to run to completion, usually without removing biomass and products during the process.

bathochromic *(in absorption spectroscopy)* describing a shift of an absorption band in the direction of longer wavelengths. *Compare* **hypsochromic**.

batrachotoxin a steroidal alkaloid neurotoxin from the skin of Colombian arrow-poison frogs of genus *Phyllobates*. It is the most potent known venom. It binds specifically to the voltage-gated sodium channel and renders the membrane permeable to sodium ions. *Compare* **tetrodotoxin**, which reverses its depolarizing effect.



batroxobin *see* **venombin**.

Batten's disease *see* **H^+-transporting ATP synthase**.

batyl alcohol 1-*O*-octadecyl-*sn*-glycerol; 3-octadecyloxy-1,2-propanediol; a hydrolysis product of **ether lipids**.

bay region a concave exterior region, bordered by three phenyl rings, of a polycyclic aromatic hydrocarbon when an angularly fused terminal benzo-ring is present. For example, the sterically hindered area between carbon atoms 4 and 5 of phenanthrene, between carbon atoms 1 and 12 of benz[*a*]anthracene, or between carbon atoms 10 and 11 of benzo[*a*]pyrene. It has been suggested that dihydrodiol epoxides in the bay region of such compounds may be responsible for their mutagenicity and carcinogenicity. *See also* **A region**, **B region**, **K region**, **L region**.

B cell **1** *or (formerly)* **beta cell** the principal cell (60–80%) of the islets of Langerhans of the pancreas. It produces, stores (as B granules), and secretes the hormone **insulin**. **2** *an alternative name for* **B lymphocyte**.

B-cell activation factor *abbr.*: BAF; *an alternative term for* **interleukin 1**.

B-cell antigen receptor complex a complex consisting of membrane immunoglobulin associated non-covalently with two proteins known as mb-1 (*other names*: Igα, CD79a) and B29 (*other names*: Igβ, CD79b) that binds antigen and initiates B-cell transformation. mb-1 and B29 are often designated α and β respectively, and the complex consists of $Ig(\alpha\beta)_2$. Signalling occurs by activation of tyrosine kinases of the Src family (lyn, blk, fyn, or lck). α and β are themselves phosphorylated on activation. All five immunoglobulin isotypes (IgG, IgM, IgD, IgA, IgE) bind two α/β heterodimers and use a similar signalling pathway, but the glucosylation of the α chain differs according to the isotype with which it associates. Examples (both precursors) from mouse: α chain, database code C79A_MOUSE, 220 amino acids (24.23 kDa); β chain, database code C79B_MOUSE, 228 amino acids (25.70 kDa).

B-cell differentiation factor *abbr.*: BDF; *an alternative term for* **interleukin 1**.

BCG *abbr. for* bacille Calmette–Guérin; the bacillus from which is made a vaccine composed of live bovine-strain tubercle bacilli, *Mycobacterium bovis*, attenuated by long cultivation on a potato–glycerol–bile medium. [After Léon Charles Albert Calmette (1863–1933), French physician and bacteriologist, and Camille Guérin (1872–1961), French veterinary surgeon and bacteriologist, who described its preparation in 1908.]

B chain **1** the longer of the two polypeptide chains of **insulin**, containing 30 amino-acid residues. **2** the **light chain** of an immunoglobulin.

B chromosome any of a heterogeneous group of accessory, extra, or supernumerary chromosomes found in many species of animals and plants. They differ from normal, or A chromosomes, by being usually smaller and frequently heterochromatic and telocentric, without great effect on the phenotype of their carriers. Both their numbers and their meiotic and mitotic behaviour are highly variable.

BCKDH *abbr. for* branched-chain α-keto acid dehydrogenase.

BCL any of several genes associated with B-cell leukemia and lymphoma. *BCL1* is identical to the gene for human **cyclin** D1; its product activates $p34^{cdc2}$ kinase and is phosphorylated in G_1 of the cell cycle; database code CGD1_HUMAN, 295 amino acids (33.73 kDa). *BCL2* is a protooncogene encoding a growth factor that prolongs survival of hematopoietic cells; its product is a mitochondrial inner membrane protein, is able to block **apoptosis**, and if overexpressed with Myc counteracts the oncogenic action of Myc. Its product exists in two forms, BCL-2 α and β, resulting from differential splicing and expressed in B-cell leukemias and lymphomas. Example α (human): database code BC2A_HUMAN, 239 amino acids (26.24 kDa). *BCL3* encodes a probable transcription factor of the I-κB family; database code BCL3_HUMAN, 446 amino acids (46.80 kDa).

BCR a human gene named after **breakpoint cluster region**, a chro-

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mosomal region found in humans and other species. It is a member of a small gene family coding for a protein with protein serine/threonine kinase activity, widely expressed in human hematopoietic and nonhematopoietic cell lines; database code BCR_HUMAN. *See also* ***abl***, **Philadelphia chromosome**.

BDF *abbr. for* B-cell differentiation factor interleukin (*see* **interleukin**).

B-DNA *abbr. for* B form of DNA.

BDNF *abbr. for* brain-derived neurotrophic factor.

Be *symbol for* beryllium.

Beadle, George Wells (1903–89), US geneticist notable in particular for formulating the one gene–one reaction hypothesis; Nobel Laureate in Physiology or Medicine (1958) jointly with E. L. Tatum 'for their discovery that genes act by regulating definite chemical events' [prize shared with J. Lederberg].

Beckmann thermometer a sensitive mercury-in-glass thermometer used for measuring small differences or changes of temperature. [After Ernst Otto Beckmann (1853–1923), German chemist.]

Becquerel, Antoine Henri (1852–1908), French physicist; Nobel Laureate in Physics (1903) 'in recognition of the extraordinary services he has rendered by his discovery of spontaneous radioactivity' [prize shared with M. Curie and P. Curie].

becquerel *symbol*: Bq; the SI derived unit of (radioactive) **activity** (def. 2) of a radionuclide; it corresponds to one **nuclear transformation** per second; i.e. 1 Bq = 1 disintegration s^{-1}. *See also* **curie**: 1 Ci = 3.7×10^{10} Bq or 1 Bq = 2.70×10^{-11} Ci.

bed volume in column chromatography, the total volume of material, both solid and liquid, in the column; i.e. the volume of the support particles plus the **void volume**. It is synonymous with **column volume** for a packed column.

Beer–Lambert law *or* **Beer–Lambert–Bouguer law** *or* **Lambert–Beer law** a combination of **Beer's law** (def. 1) and **Lambert's law**; put into modern terms, it states that the **absorbance**, A, of a beam of collimated monochromatic radiation in a homogeneous isotropic medium is proportional to the absorption pathlength, l, and to the amount-of-substance concentration, c, (or, in the gas phase, to the pressure) of the absorbing species. The law may be expressed by the relations

$$A = \lg (\Phi_0/\Phi) = \varepsilon c l \text{ or } \Phi = \Phi_0 = 10^{-\varepsilon c l}$$

where Φ_0 and Φ are respectively the **spectral powers** of the incident and transmitted radiation beams, and the proportionality constant, ε, is the molar (decadic) absorption coefficient – *see* **absorption coefficient**.

Beer's law **1** *or (sometimes)* **Bouguer–Beer law**; a physical law extending **Bouger's law** to solutions: it states that when light passes through a given thickness of an absorbing solution of concentration c, the intensity of the transmitted light, I_{trs}, decreases exponentially as c increases linearly. It may be expressed as $I_{trs} = I_0\, e^{-kc}$, where I_0 is the intensity of the incident light and k is a constant. The law applies in practice only to monochromatic light (or other electromagnetic radiation) and when factors such as reflection or scattering are negligible or can be corrected for. *See also* **Beer–Lambert law**. [After August Beer (1825–63), German physicist who formulated it in 1857.] **2** name commonly but incorrectly applied to **Beer–Lambert law**

beet sugar *an alternative name for* **sucrose** when this has been extracted from sugar beet.

Beh *symbol for* the behenoyl group.

behenoyl *symbol*: Beh; *trivial name for* docosanoyl, CH_3–$[CH_2]_{20}$–CO–, the acyl group derived from the aliphatic acid behenic acid (= docosanoic acid), which occurs naturally in animal tissues and most seed fats.

bek a gene related to that for the **fibroblast growth factor** (FGF) receptor. Named after bacterial expressed kinase, it encodes a plasma membrane protein tyrosine kinase of class IV with an insert in the kinase region that binds FGFA with high affinity; database code Hsfgfrbe.

Benacerraf, Baruj (1920–), Venezuelan-born US immunologist notable for his discovery of histocompatability genes and their role in regulation of the immune response; Nobel Laureate in Physiology or Medicine (1980) jointly with J. Dausset and G. D. Snell 'for their discoveries concerning genetically determined structures on the cell surface that regulate immunological reactions'.

Bence-Jones protein any of a group of **myeloma proteins**, occurring in the urine of patients with multiple myelomatosis and related conditions, that precipitate on heating the urine to 60 °C, but redissolve at higher temperatures. They consist of light chains of **immunoglobulins** synthesized by the myeloma cells. Example, a kappa chain: database code KV1K_HUMAN, 108 amino acids (11.27 kDa). [After Henry Bence-Jones (1813–73), English physician who described them in 1847.]

Benedict's solution **1 Benedict's qualitative solution**, a reagent used to test for the presence of glucose and other reducing sugars. It contains 0.07 M copper sulfate, 0.67 M sodium citrate, and 0.94 M sodium carbonate. When heated with reducing sugars it is reduced and a red precipitate of cuprous oxide is formed. **2 Benedict's quantitative solution**, a reagent used in the estimation of glucose and other reducing sugars. It contains 0.072 M copper sulfate, 0.7 M sodium carbonate, 1.29 M potassium thiocyanate, and a trace of potassium ferrocyanide. On boiling, 25 ml of this solution is reduced by 50 mg glucose. Other reducing sugars may be estimated similarly. [After Stanley Rossiter Benedict (1884–1936), US biochemist.]

benign describing a neoplasm that is harmless, localized, and nonmetastasizing, although it may physically impede the function of a nerve or muscle.

bentonite a colloidal, native hydrated aluminium silicate clay consisting principally of montmorillonite, a complex aluminosilicate, $Al_2O_3{\cdot}4SiO_2{\cdot}H_2O$, which has marked adsorptive properties. It is used as an inhibitor of nucleases and also in the **bentonite flocculation test**, a passive agglutination test in which antigen-coated bentonite particles are used to detect specific antibody.

benzidine *trivial name for* 4,4′-diaminobiphenyl, a substance that is carcinogenic for humans. It was formerly used in a highly sensitive test for the presence of blood, giving a green or blue colour in acetic acid solution on addition of hydrogen peroxide. Another former application was in the chromogenic assay of peroxidases. In view of the carcinogenicity, it has been replaced by **2,7-diaminofluorene** and other compounds.

benzo+ *or (sometimes before a vowel)* **benz+** *comb. form* **1** denoting the fusion of a benzene ring to a cyclic organic molecule. **2** indicating derivation from benzene or benzoic acid; *compare* **phenyl**.

benzoate 1,2-dioxygenase EC 1.14.12.10; *systematic name*: benzoate,NADH:oxygen oxidoreductase (1,2-hydroxylating, decarboxylating); *other name*: benzoate hydroxylase. A bacterial dioxygenase that is involved in the utilization of aromatic compounds. It catalyses a reaction between benzoate, NADH, and dioxygen to form catechol, CO_2, and NAD^+. Iron is a cofactor. Example from *Acinetobacter calcoaceticus*: this comprises three subunits, two of which, α and β, represent the hydroxylase, while the third, γ, is an electron-transport flavoprotein; α subunit: database code BENA_ACICA, 461 amino acids (52.01 kDa); β subunit (probably involved in substrate specificity): database code BENB_ACICA, 169 amino acids (20.05 kDa); γ subunit (similar to ferredoxin reductase with 2Fe–2S motifs): database code BENC_ACICA, 348 amino acids (38.74 kDa).

benzodiazepine *abbr.*: BZ; **1** 2*H*-1,4-benzodiazepine; a bicyclic compound consisting of a benzene ring fused to a seven-membered partially unsaturated ring containing two nitrogen atoms. **2** any member of a large class of pharmacologically active substances containing the benzodiazepine ring system. They are CNS depressants of low toxicity, having sedative and anxiolytic effects. A number are useful therapeutically; one of the most widely used is **diazepam** (*one proprietary name*: Val-

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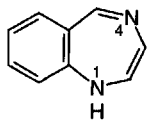
ium). Specific high-affinity **benzodiazepine binding sites** are present in the CNS. They have been classified as BZ_1, primarily associated with anxiolytic effects, and BZ_2. It has been suggested that the effects of benzodiazepines are mediated through enhancement of the inhibitory action of GABA on the brain, and they are known to modulate the effects of GABA at **$GABA_A$ receptors**. Cloning studies of the $GABA_A$ receptor subunits have indicated that the γ subunit confers benzodiazepine sensitivity, and that the combination of different subunit types affects the receptor specificity, the presence of α1 subunits in the complex conferring BZ_1 pharmacology.



1*H* form

benzodiazepine inverse agonist a drug or other compound that binds to benzodiazepine receptors but has effects that are the opposite of those produced by a benzodiazepine agonist, i.e. it causes anxiety and convulsions.

***o*-benzoquinone** 3,5-cyclohexadiene-1,2-dione; 1,2-benzoquinone; *o*-quinone. The oxidized form of **pyrocatechol**.

***p*-benzoquinone** 2,5-cyclohexadiene-1,4-dione; 1,4-benzoquinone; (*p*-)quinone. The oxidized form of **hydroquinone**. *See also* **quinhydrone**.

benzoyl *symbol*: Bz *or (preferably)* PhCO; the C_6H_5–CO– group; the acyl group derived from benzoic (= benzenecarboxylic) acid.

benzyl *symbol*: Bzl *or (preferably)* $PhCH_2$; the C_6H_5–CH_2– group; the alkyl group derived from benzyl alcohol (= benzenemethanol).

benzyloxycarbonyl *or (formerly)* **carbobenzoxy** *or* **carbobenzyloxy** *symbol*: Z *or* Cbz; the C_6H_5–CH_2–O–CO– group, which is introduced into amino groups of peptides and proteins with reagents such as *N*-(benzyloxycarbonyloxy)succinimide.

Berg, Paul (1926–), US biochemist and molecular geneticist distinguished for his discovery of a means of introducing foreign DNA into bacteria by the use of viruses as vectors; Nobel Laureate in Chemistry (1980) 'for his fundamental studies of the biochemistry of nucleic acids, with particular regard to recombinant-DNA' [prize shared with W. Gilbert and F. Sanger].

Bergström, Sune K. (1916–), Swedish biochemist notable for his isolation and purification of prostaglandins; Nobel Laureate in Physiology or Medicine (1982) jointly with B. I. Samuelsson and J. R. Vane 'for their discoveries concerning prostaglandins and related biologically active substances'.

beriberi a disease due to thiamine (vitamin B_1) deficiency and characterized by degenerative changes in the peripheral nerves, digestive system, and heart accompanied by edema.

Berkfeld filter a (candle) filter, made of diatomaceous earth, used to sterilize solutions. The pore size is relatively large and three porosities are graded V, N, and W (German *viel*, *normal*, and *wenig*) corresponding to coarse, normal, and fine. [After Wilhelm Berkefeld (1836–97), German chemist and manufacturer (the owner of the mine at Kieselguhr, where the earth was mined for production of the filter).]

Bernal chart a means of specifying the position of a spot on an X-ray diffraction photograph by two coordinates. [After John Desmond Bernal (1901–71), British crystallographer who described it in 1926.]

Bernard–Soulier syndrome *see* **von Willebrand factor**.

Bes *or* **BES** *abbr. for* 2-[bis(2-hydroxyethyl)amino]ethanesulfonic acid; a **Good buffer substance**, pK_a (20 °C) = 7.15.

Best, Charles Herbert (1899–1978), Canadian physician and physiologist notable for discovering the enzyme histaminase and the lipotropic action of choline but particularly for his role (when a research student) in the discovery (with F. G. Banting) of a means of extracting the hormone insulin from pancreatic tissue and demonstrating its antidiabetic efficacy; this achievement was duly recognized by Banting by dividing his share of the Nobel prize with Best.

beta *symbol*: β (lower case) *or* B (upper case); the second letter of the Greek alphabet. For uses *see* **Appendix A**.

beta adrenergic *or* **β adrenergic** *see* **adrenergic**.

beta adrenoceptor *or* **β adrenoceptor** *see* **adrenoceptor**.

beta barrel *or* **β barrel** a molecular configuration, more strictly known as an **antiparallel β barrel**, that occurs in the structure of globular proteins. It is characterized by crossing of the beta strands in such a way that the central regions of the strands are buried away from the solvent.

beta bend *or* **beta turn** *or* **β bend** *or* **β turn** a short stretch of polypeptide chain that allows the main direction of the chain to change. It consists of four amino-acid residues in which the CO group of residue *n* is hydrogen bonded to the NH group of residue *n* + 3.

beta blockade the process of inhibiting beta adrenoceptors with an antagonist.

beta blocker an antagonist of beta adrenoceptors.

beta cell *or* **β cell** *(formerly) an alternative name for* **B cell** (def. 1).

beta-cell tropin *or* **β-cell tropin** a peptide fraction obtained from the *pars intermedia* of mouse pituitary that stimulates insulin secretion by perfused rat pancreas or isolated pancreatic islets. It is immunochemically related to, but separable from, **corticotropin-like intermediary lobe peptide**.

betacellulin a potent mitogenic glycoprotein with EGF-like domains, purified from the conditioned medium of mouse pancreatic beta tumour cells, retinal pigment epithelial cells, and vascular smooth muscle cells. It may play a role in the vascular complications associated with diabetes. The C-terminal region shows 50% homology with rat **transforming growth factor** α. The precursor is a type I **membrane protein**, and the mature form is a secretory protein. Example (precursor) from human: database code BTC_HUMAN, 178 amino acids (19.72 kDa).

beta configuration *or* **β configuration** a stable configuration of a polypeptide chain in which the chain is almost fully extended but slightly puckered and is hydrogen bonded to an adjacent polypeptide chain, thus forming a **beta strand**, the axial distance between adjacent amino-acid residues being ≈ 0.35 nm; the adjacent chains may be either **parallel** (running in the same direction) or **antiparallel** (running in opposite directions).

betacyanin *see* **betalain**.

beta decay *or* **β decay** decay of a radionuclide by the emission of a **beta particle**.

beta emitter *or* **β emitter** any nuclide that emits either positive or negative beta particles.

beta globulin *or* **β globulin** any of a diverse group of **plasma proteins**, including lipoproteins and transferrin, that migrate slower than the **alpha globulins** during electrophoresis at slightly alkaline pH values.

beta granin *or* **β granin** *see* **chromogranins**.

beta granule *an alternative name for* **B granule**.

beta helix *or* **β helix** a configuration of a polypeptide chain in which each amide group forms hydrogen bonds with the carbonyl group of a residue on average 22 residues removed from it along the chain. The translation along the helix for each residue (the 'pitch') is 0.22 Å and for each turn is 4.8 Å, with 22 residues per turn. The diameter of the helix is thus large (about 27 Å) with a 22 Å hole through the centre of the helix.

beta hemolysis *or* **β hemolysis** a type of hemolysis, characteristic of certain strains of streptococci, in which a clear zone is formed around the bacterial colonies when cultured on a blood agar plate. *Compare* **alpha hemolysis**.

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betaine the *N*-trimethyl derivative of an amino acid; the term originally denoted **N-trimethylglycine**, now called **glycine betaine**. Glycine betaine acts as a methyl-group donor in some reactions; *see*, e.g., **betaine–homocysteine *S*-methyltransferase**.

betaine-aldehyde dehydrogenase EC 1.2.1.8; an enzyme involved in the formation of **betaine**. It catalyses the reaction:

betaine aldehyde + NAD^+ + H_2O = betaine + NADH.

Example from *Escherichia coli*: database code DHAB_ECOLI, 489 amino acids (52.72 kDa).

betaine–homocysteine *S*-methyltransferase EC 2.1.1.5; an enzyme that catalyses the reaction:

trimethylammonioacetate (glycine **betaine**) + L-homocysteine = dimethylglycine + L-methionine.

beta-lactoglobulin *or* **β lactoglobulin** the principal protein of ruminant milk whey, constituting 50–60% of total whey. It is present as a dimer, M_r ~ 36 000, pI 5.2. Of unknown function, it binds retinol and is a member of the **lipocalin** family. It occurs in milk of other species (e.g. horse), but not human. Analogues occur in marsupial milk. Example (precursor) from *Bos taurus*: database code LACB_BOVIN, 178 amino acids (19.88 kDa). *See also* **lactalbumin** (def. 1).

betalain any of a group of coloured alkaloids occurring widely in plants of the order Centrospermae. They are divided into two groups, **betacyanins** and **betaxanthins**, and both occur in plant vacuoles. The former impart a red-violet colour and the latter a yellow colour to the plant organs that contain them.

beta lipoprotein *or* **β lipoprotein** any of the plasma lipoproteins that behave electrophoretically as **beta globulins**, but normally designated **low density lipoprotein**. *See also* **plasma protein**.

beta oxidation *or* **β oxidation** the metabolic oxidation of a long-chain fatty acid by successive cycles of reactions during each of which the fatty acid is shortened by a two-carbon-atom fragment removed as acetyl coenzyme A. The name derives from the fact that the β-carbon atom is the point of oxidation. *See also* **beta-oxidation system**, **Knoop's hypothesis**.

beta-oxidation system a mitochondrial complex that carries out the reactions of beta oxidation. It contains enzymes that fall into the following four categories:

(1) Acyl-CoA dehydrogenases; these include:

(a) **long-chain-acyl-CoA dehydrogenase** (*abbr.*: LCAD) EC 1.3.99.13; this catalyses a reaction between acyl-CoA and electron transferring flavoprotein (ETF) to form 2,3-dehydroacyl-CoA and reduced ETF; FAD is a cofactor. Examples: a mitochondrial matrix protein and a homotetramer, having three isoenzymes with different substrate specificities; deficiency is associated with nonketotic hypoglycemia; precursor (including transit peptide): database code ACDL_HUMAN, 430 amino acids (47.62 kDa);

(b) **acyl-CoA dehydrogenase** is the corresponding medium-chain-specific enzyme, (*abbr.*: MCAD) EC 1.3.99.3; database code ACDM_HUMAN, 421 amino acids (46.54 kDa); and

(c) **butyryl-CoA dehydrogenase** is the short-chain enzyme (*abbr.*: SCAD) EC 1.3.99.2; database code ACDS_HUMAN, 412 amino acids (44.25 kDa).

Both of the latter have corresponding activities and the same subunit composition as LCAD. Deficiencies in MCAD and SCAD are associated with fasting hypoglycemia, hepatic dysfunction, and encephalopathy (often fatal) for the former, and adult lipid storage myopathy and infant acidosis and muscle weakness.

(2) **enoyl-CoA hydratase** EC 4.2.1.17; this catalyses a reaction forming (3*S*)-3-hydroxyacyl-CoA from *trans*-2(or 3)-enoyl-CoA, hydrating the double bond introduced by the enzymes in category 1. Example (rat, precursor): database code ECHM_RAT, 290 amino acids (31.48 kDa); it is a homohexamer and a mitochondrial matrix protein.

(3) **3-hydroxyacyl-CoA dehydrogenase** EC 1.1.1.35; this catalyses the oxidation of (3*S*)-3-hydroxyacyl-CoA by NAD^+ to 3-oxoacyl-CoA with formation of NADH. Example from pig: database code HCDH_PIG, 307 amino acids (33.24 kDa); it is a homodimer and mitochondrial matrix protein.

(4) **3-ketoacyl-CoA thiolase** (*see* **thiolase**). Example from rat: database code THIM_RAT, 397 amino acids (41.82 kDa); a homotetramer and mitochondrial protein.

beta particle *or* **β particle** either a (negatively charged) electron or a (positively charged) positron emitted in the **transformation** (def. 5) of a radionuclide.

beta-pleated sheet *or* **β-pleated sheet** *another name for* **beta sheet.**

beta radiation *or* **β radiation** an emission of **beta particles**.

beta receptor *or* **β receptor** *see* **adrenoceptor**.

beta sheet *or* **β sheet** *or* **β-pleated sheet** an approximately planar array of two or more **beta strands**.

beta strand *or* **β strand** one of the two basic elements of the **secondary structure** adopted by a polypeptide chain within the hydrophobic core of a globular protein (*see also* **alpha helix**). It consists of two chains in a **beta configuration**. Two or more strands may interact to form a **beta sheet**.

beta structure *or* **β structure** any part of the structure of a protein molecule consisting of one or more β strands.

beta turn *or* **β turn** *an alternative name for* **beta bend**.

betaxanthin *see* **betalain**.

B form of DNA *abbr.*: B-DNA *or* DNA-B; the molecular conformation adopted by fibres of the sodium salt of duplex DNA at high relative humidity and in aqueous solution. It consists of a right-handed double helix containing about ten nucleotide residues per turn with the planes of the base pairs normal to the axis of the helix. It is the basis of the **Watson–Crick model of DNA**, and is thought to resemble the conformation of most of the DNA *in vivo*. *See also* **A form** (def. 1), **C form**, **Z form**.

B/F ratio *abbr. for* bound-to-free ratio (in ligand binding). A plot of the B/F ratio versus the concentration of free ligand is known as a **Scatchard plot**.

BGG *abbr. for* bovine gamma globulin; the component of bovine serum represented by fraction II of a **Cohn fractionation**.

B granule *or* **beta granule** any of very numerous membrane-bound vesicles (granules) containing stored insulin that are found in the **B cells** of the pancreatic islets. The granules stain a deep bluish purple with Gomori's aldehyde fuchsin and Ponceau stain.

bhang *see* **cannabis**.

BHK cell *abbr. for* baby hamster kidney cell; a cultured cell derived from this organ.

BHT *abbr. for* butylated hydroxytoluene, di-*tert*-butyl-*p*-cresol, an **antioxidant**.

bi+ **1** *comb. form* meaning two, twice, or double. **2** *prefix* (in organic chemical nomenclature) indicating two identical groups or rings joined by a link; e.g. biacetyl, biphenyl. **3** *prefix* (in inorganic chemical nomenclature) signifying an acid salt of a dibasic acid; e.g. sodium bicarbonate (though now more correctly termed sodium hydrogencarbonate). **4** *(in enzymology)* denoting two kinetically important substrates and/or products of an enzymic reaction (*see* **reactancy of enzymes**). *See also* **bis+**, **di+**.

Bi *symbol for* bismuth.

BIAcore *proprietary name* of an optical biosensor instrument that measures refractive index changes to record in real-time interactions of macromolecules with ligands immobilized on a dextran-coated gold surface. The resulting 'sensorgrams' can be used to derive kinetic parameters of the interactions.

bialaphos a linear tripeptide produced as a secondary metabolite by *Streptomyces hygroscopicus*. The structure is PT-Ala-Ala, where PT is the glutamate analog, phosphinothricin. After hydrolysis of bialaphos by intracellular nonspecific peptidases, PT acts as an inhibitor of **glutamate-ammonia ligase** (glutamine synthetase), and thereby derives herbicide and antibiotic activities.

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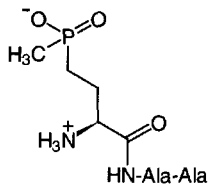


bialaphos

Bial's test a colorimetric test for aldopentoses. *See* **orcinol test**. [After Manfred Bial (1870–1908), German physician.]

bibrotoxin a vasoconstrictor peptide of the **endothelin/sarafotoxin** family, isolated from the venom of the burrowing wasp *Atractaspis bibroni*. The sequence,

CSCADMTDKECLYFCHQDVIW,

is identical to that of sarafotoxin B except that Ala[4] replaces Lys[4].

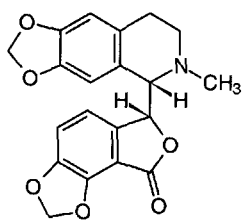
bicarbonate the HCO_3^- ion; now more correctly termed hydrogencarbonate.

bichromatic analysis a term sometimes used to describe any analytical method involving observation at two wavelengths.

Bicine *or* **BICINE** *abbr. for N,N*-bis(2-hydroxyethyl)glycine; a **Good buffer substance**; pK_a (20 °C) = 8.35.

bicoid protein a segment-polarity protein, discovered in *Drosophila*, that provides positional cues for the development of head and thoracic segments. It regulates the expression of zygotic genes, possibly through its **homeodomain**, and inhibits the activity of other maternal gene products. It forms an anterior–posterior gradient in the embryo and acts as a transcriptional activator. It binds to *caudal* mRNA. There is similarity to other **paired**-type homeobox proteins. Example from *Drosophila melanogaster*: database code HMBC_DROME, 494 amino acids (54.43 kDa).

bicuculline 6-(5,6,7,8-tetrahydro-6-methyl-1,3-dioxolo[4,5-*g*]isoquinolin-5-yl)furo[3,4-*e*]-1,3-benzodioxol-8(6*H*)-one; a naturally occurring alkaloid with several sources, including *Dicentra cucullaria* and *Adlumia fungosa*. It is a potent convulsant with effects probably mediated by its GABA antagonist activity at **$GABA_A$ receptors**.



bidentate **1** having two teeth or two toothlike processes. **2** describing a **ligand** molecule that chelates a metal ion by means of two donor atoms.

bifunctional having two functions.

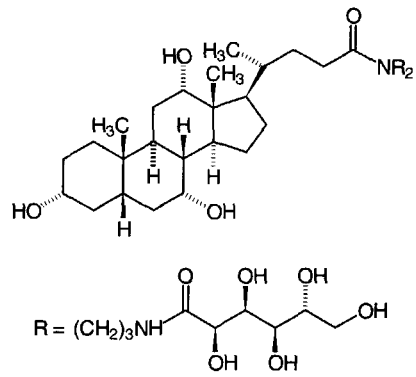
bifunctional antibody an antibody having two combining sites for antigen.

bifunctional catalyst a catalyst that provides both acidic and basic catalytic functions.

bifunctional reagent a compound with two reactive functional groups that can interact with two groups in one molecule or with one group in each of two different molecules.

big-big gastrin *or* **big gastrin** *see* **gastrin**.

BigCHAP *N,N*-bis(3-D-gluconamidopropyl)cholamide; a non-ionic detergent analogue of **CHAPS**, but with reduced electrostatic properties; aggregation number 10, CMC 3.4 mM.



big gastrin *see* **gastrin**.

big glucagon *or* **big plasma glucagon** material that is separable from normal human plasma and shows glucagon-like immunoreactivity. It has an estimated M_r of 160 000.

biglycan bone and cartilage proteoglycan I precursor; a connective tissue glycoprotein of the extracellular matrix related to **decorin** and fibromodulin. Example (precursor) from human: database code PGS1_HUMAN, 368 amino acids (41.61 kDa).

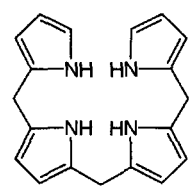
bijou bottle a small glass screw-capped bottle of 5–7 ml capacity, used especially for liquid and solid cultures.

bikunin a plasma glycoprotein found both in the free state and complexed with the heavy chains of the inter-α-inhibitor family, forming the light chain. It is a serine protease inhibitor having a tandem arrangement of Kunitz domains; it may participate in the control of events such as endothelial cell growth and oocyte cumulus expansion and stabilization. It is synthesized from an α_1-microglobulin/bikunin precursor. Example from human: database code HC_HUMAN, 352 amino acids (38.96 kDa); residues 20–203 form α_1-microglobulin and 206–352 form inter-α-trypsin inhibitor light chain (the inhibitory subunit).

biladiene *the semisystematic name for* either of two linear tetrapyrroles in which the carbon bridges contain two more double bonds than **bilane** i.e. two of the three carbon bridges in the molecule are methine groups.

bilamellar having two **lamellae**; formed of two plates.

bilane *the systematic name for* a linear tetrapyrrole in which each of the three carbon bridges linking the pyrrole nuclei is saturated, i.e. is a methylene group, and in which, unless otherwise specified, each of the four nitrogen atoms also is saturated. It is the fundamental structure for the naming of linear tetrapyrroles, is defined without oxygen substituents, and is numbered (omitting C_{20}) to agree with the numbering of the unsubstituted porphyrin ring system. *Trivial name*: bilinogen.



bilateral hydrophobic zippers putative α-helical segments of the acidic ribosomal proteins, A1, A2, L44′, and L45, of *Saccharomyces cerevisiae*. They have two arrays of 5–7 hydrophobic residues on opposite sides. *Compare* **leucine zipper**, **bZIP**.

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bilatriene *an alternative (less-favoured) name for* **bilin**.

bilayer a layer that is two molecules thick, as in some membranes. *See* **lipid bilayer**, **unit membrane**.

bilayer lipid membrane *see* **black lipid membrane**.

bile a secretion produced by the vertebrate liver and conveyed through the bile duct to the duodenum. Its alkaline nature helps to neutralize acidic gastric secretions passing from the stomach, and the **bile salts** it contains are involved in the digestion of fat. Bile also serves as a medium for the excretion of various substances, notably cholesterol (either as such or in the form of bile salts to which it is converted), pigments (from hemoglobin breakdown), heavy metals, and other waste products (usually of >400 Da).

bile acid any member of a group of steroid carboxylic acids occurring in bile, where they are present as the sodium salts of their amides with glycine or taurine (*see* **bile salt**). The C_{24} acids are hydroxy or keto derivatives of cholanic or allocholanic acids; some C_{27} bile acids are known in eutherian mammals. In mammals, the C_{24} acids are found conjugated with glycine (*see* **glycocholate**) as well as with taurine (*see* **taurocholate**); in the rest of the animal kingdom only taurine conjugates have been found.

bile alcohol any of a group of polyhydroxy derivatives of **cholestane**, present as their sulfuric acid esters in the bile of amphibians and some fishes.

bilene *the semisystematic name for* either of two tetrapyrroles in which the carbon bridges contain one more double bond than **bilane**; i.e. one of the three bridges in the molecule is a methine group.

bile pigment any bilirubinoid pigment present in bile; i.e. any linear tetrapyrrole derived from a **porphyrin** (which is a cyclic tetrapyrrole). For physiological reasons certain dipyrroles are also sometimes regarded as bile pigments.

bile salt the sodium salt of the conjugate of any **bile acid** with either glycine or taurine. Bile salts are potent surfactants; in the gut they emulsify ingested lipid, promote its hydrolysis by the activation of lipases, and facilitate its absorption, thereafter being excreted in the feces. *See also* **glycocholate**, **taurocholate**.

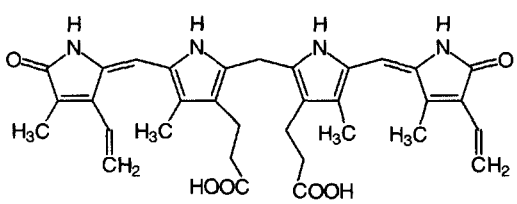
biliary of or relating to **bile**.

bilin **1** *the systematic name for* the linear tetrapyrrole in which the carbon bridges contain three more double bonds than **bilane**; i.e. all three bridges are methine groups. This name is preferred to bilatriene. **2** any coloured **bile pigment** formed by the oxidation of a colourless bile pigment, or **bilinogen** (def. 2). Thus the bilinogens urobilinogen and stercobilinogen form urobilin and stercobilin, respectively, on oxidation.

bilinogen **1** *trivial name for* bilane. **2** any colourless **bile pigment** that may be oxidized to a coloured bile pigment (*see* **bilin** (def. 2)).

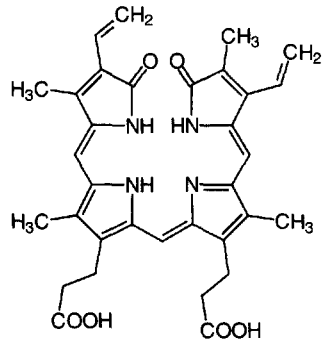
biliprotein *an alternative name for* **phycobiliprotein**.

bilirubin *or (formerly)* **bilirubin IXα** *the recommended trivial name for* the linear tetrapyrrole 8,12-bis(2-carboxyethyl)-2,7,13,17-tetramethyl-3,18-divinylbiladiene-*ac*-1,19(21*H*,24*H*)-dione. It is produced in the reticuloendothelial system by the reduction of **biliverdin** and transported to the liver as a complex with serum albumin. In the liver, bilirubin is rendered water-soluble by conjugation of the carboxyethyl side-chains to form bilirubin bisglucuronide, most of which is excreted in the bile. Bilirubin accumulates in the blood and tissues in jaundice.



bilirubin oxidase EC 1.3.3.5; an enzyme that catalyses the oxidation by dioxygen of bilirubin to biliverdin and H_2O. Example from the fungus *Myrothecium verrucaria*: database code B48521, 572 amino acids (63.88 kDa).

biliverdin *or (formerly)* **biliverdin IXα** *the recommended trivial name for* the linear tetrapyrrole 8,12-bis(2-carboxyethyl)-2,7,13,17-tetramethyl-3,18-divinylbilin-1,19(21*H*,24*H*)-dione. It is formed in the reticuloendothelial system by the first step in heme degradation, catalysed by heme oxygenase (decyclizing), EC 1.14.99.3, a reaction in which the α-methene group of heme is oxidized to carbon monoxide. Biliverdin is then reduced by biliverdin reductase, EC 1.3.1.24, to **bilirubin**.



biliverdin reductase EC 1.3.1.24; an enzyme that catalyses the reaction of bilirubin with NAD(P)$^+$ to form biliverdin and NAD(P)H. Example from human: database code PN0159, 204 amino acids (21.83 kDa).

bimodal *(in statistics)* distribution with two **modes**.

bimolecular having a **molecularity** of two; relating to, consisting of, or involving two molecular entities.

bimolecular layer a layer that is two molecules thick.

bimolecular reaction any chemical reaction in which there is a transition state composed of the atoms of two separate molecular entities, which may be the same or different.

binal double; twofold.

binary **1** consisting of or forming two things or parts; dual. **2** describing a number system having the numeral 2 as its **base** (def. 4b). *See also* **bit**.

binary compound a compound consisting of only two chemical elements; e.g. ammonia, sodium chloride, water.

binary digit *see* **bit**.

binary fission the reproduction of a living cell by division into two equal, or near-equal, parts.

binary operator any arithmetic or logical operator (e.g. +, AND, OR) that operates on two quantities.

binary representation a notation by which **alphanumeric** symbols are represented by two digits, 0 and 1, in a known sequence. The displacement of one digit position to the left denotes multiplication by a power of 2.

binder protein I *see* **cortisol metabolite binding protein (large)**.

bindin a protein of 285 amino acids, M_r 35 000, extracted from the insoluble granular material of sea-urchin sperm, responsible for the attachment of the sperm to the vitelline layer of the egg. Bindins may mediate the species-specific recognition of eggs by sperm. *See also* **spermadhesin**, **zona pellucida sperm-binding protein**.

binding the act or process by which one molecule attaches to another by noncovalent forces; ligation *see* **ligate** (def. 3). *See* **ligand**. *See also* **binding site**.

binding assay *an alternative term for* **saturation analysis**.

binding capacity a measure of the quantity of ligand or the number of ligand molecules that can be bound by a given amount of a particular binding agent or system.

binding constant *an alternative term for* **affinity constant**.

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binding curve any graphical representation of the extent of binding between two compounds at varying relative concentrations of the reactants.

binding energy the free energy change accompanying the binding of n_i ligand molecules to a macromolecule to produce a particular configuration of the liganded macromolecule.

binding fraction *an alternative term for* **saturation fraction**.

binding potential *symbol*: Π; a concept introduced to clarify the definition of linked functions, linkage groups, and linked sites in ligand binding. It is defined by: $\nu_i = \delta\Pi/\delta\mu_i$ where ν_i is the ratio of component i to that of a reference component and μ_i is the chemical potential of i.

binding protein *abbr.*: BiP; a **luminal protein** of the endoplasmic reticulum that is a member of the hsp70 family of **heat-shock proteins** and is a typical **molecular chaperone**. It recognizes incorrectly folded proteins as well as protein subunits that have not yet assembled into their oligomeric complexes and facilitates their oligomerization of folding. BiP activity requires the participation of ATP, which is hydrolysed to ADP and inorganic phosphate. Example (precursor) from human: database code GR78_HUMAN, 653 amino acids (72.03 kDa); this is also known as 78 kDa glucose regulated protein.

binding set the spatially organized collection of all the groups or residues of *one* protomer that are involved in its binding to *one* other protomer.

binding site a specific region in a macromolecule or other molecular entity, or in a membrane, that takes part directly in the combination with a **ligand**. Binding sites may be independent or interacting, depending on whether or not the binding of one ligand to one site affects the binding of other ligands to other sites on the same macromolecule, or membrane. *See also* **co-operative ligand binding**.

binomial **1** a mathematical expression made up of two terms, e.g. $2x + 5y$. **2** a two-part taxonomic name (*see* **binomial nomenclature**).

binomial coefficient the coefficient of any term arising from the expansion of the algebraic binomial $(a + b)^n$.

binomial distribution a statistical function in which the probabilities that an event will or will not occur are given by the successive coefficients of a binomial expansion of the form $(a + b)^n$, where a and b are the probabilities that an event will and will not occur, respectively.

binomial nomenclature a system of naming organisms, devised by the Swedish botanist Carolus Linnaeus (1707–78), that employs two Latin names, the first being the genus and the second the species to which the organism belongs.

bio+ *comb. form* denoting life or living organisms, or systems derived from them.

bioactivation the activation of a drug or other substance in an organism or by means of a biological or biochemical system.

bioactive *an alternative term for* **biologically active**.

bioanalytical of or pertaining to biochemical analysis.

bioassay *or* **biological assay** any quantitative estimation of biologically active substances by measurement of the magnitude of their actions on living organisms or parts of organisms. It is performed under standard conditions and by reference to preparations of defined potency or activity.

bioautograph the record obtained in **bioautography**.

bioautography a method for detecting, in a complex mixture, small amounts of substances that are able to act as essential growth factors for a test organism(s). The components of the mixture are first separated by chromatography. The resulting chromatogram is then placed in contact with a culture of the test organism in a solid medium lacking a specific component. Hence, the organism will only grow where the component is present in the chromatogram, thereby establishing its presence in the original mixture.

bioavailability **1** the relative amount of the dose of a drug or other substance reaching the systemic circulation. **2** the rate and extent to which the therapeutic moiety of a drug is absorbed and becomes available to the site of drug action.

bioblast any very small mass of protoplasm having formative powers, formerly considered to be the ultimate elementary living particles; it is now thought the particles seen may have been **mitochondria**.

biocatalyst any agent, present in or obtained from living material, that can increase the rate at which a chemical reaction occurs without itself undergoing permanent change; a biological or biochemical **catalyst**. Biocatalysts are commonly **enzymes**. *See also* **ribozyme**. —**biocatalysis** *n.*

biochemical **1** of or pertaining to **biochemistry**. **2** any chemical substance occurring in or isolated from an organism.

biochemical engineering *or* **bioengineering** the scientific discipline underlying the industrial processing of biological materials, e.g. fermentation-based pharmaceuticals, foods, and effluents.

biochemical evolution the evolution of the biochemical processes and components of living organisms, such as the structure and function of biologically important molecules, metabolic pathways, subcellular structures, and cells.

biochemical genetics the branch of genetics concerned with the chemical nature of hereditary determinants and how they function at the molecular level.

biochemical imprinting the adaptive increase in enzyme activities that can occur along specified metabolic pathways when there is a large and sustained traffic through them.

biochemical lesion any biochemical change, such as the absence or inactivation of an enzyme, that diminishes the fitness of an organism or leads to a pathological condition.

biochemical marker any specific character that may be detected by a biochemical test, e.g. the presence or absence of a particular enzyme.

biochemical oxygen demand *or* **biological oxygen demand** *abbr.*: BOD; a measure of pollution of water in lakes, rivers, etc. due to the presence of organic matter. Oxidation of the latter by microorganisms removes dissolved oxygen, hence reducing the ability of the water to sustain aquatic life. BOD is the amount of oxygen (mg) taken up by a 1-litre sample of water in 5 days (BOD_5) at 20 °C in the dark; it may be necessary to add additional, uncontaminated, water to augment the amount of oxygen available. Sometimes incubation is for a longer time, e.g. 20 days, in which case it is indicated by BOD_{20}. *Compare* **chemical oxygen demand**.

biochemistry *or* **biological chemistry** the branch of science dealing with the chemical compounds, reactions, and other processes that occur in living organisms. Lehninger expressed the challenge to the biochemist as follows: 'Living things are composed of lifeless molecules. When these molecules are isolated and examined individually, they conform to all the physical and chemical laws that describe the behaviour of inanimate matter. Yet living organisms possess extraordinary attributes not shown by collections of inanimate molecules.' In this regard Horowitz has proposed a set of criteria for living systems: 'Life possesses the properties of replication, catalysis and mutability.' Biochemists are, therefore, concerned with the manner in which living organisms exhibit these properties. —**biochemist** *n.*

biochip an integrated circuit in which electrical and logical functions are performed by protein molecules appropriately manipulated.

biocide any chemical substance that kills living cells or organisms. —**biocidal** *adj.*

biocompatible compatible with life; having no injurious effect on living organisms. —**biocompatibility** *n.*

bioconversion a technique in which the enzymic apparatus of an organism is used to convert or process a chemical substance, not normally present in the organism, into another, (often commercially) useful one.

biocytin ε-*N*-biotinyl-L-lysine; a naturally occurring complex of **biotin**, found especially in autolysates of rapidly growing yeast. It is liberated from biotin holoenzymes by proteolysis.

biodegradable capable of being broken down by the action of living organisms. —**biodegradability** *n.*

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biodegradation 1 the processes by which exogenous, usually waste materials are broken down by living organisms. Sometimes this breakdown involves two or more kinds of organisms acting in cooperation. Such degradative abilities are employed to convert waste materials into more acceptable and manageable forms or to produce useful end products. 2 *an alternative term for* **catabolism**. *Compare* **biosynthesis**.

biodeterioration any undesirable change in the properties of a material brought about by the activities of organisms.

bioelectricity electric current or electric potential produced in living organisms. —**bioelectric** *adj.*

bioelectrochemistry the application of electrochemical models and techniques to biological problems.

bioelectronics the application of biomolecular principles to microelectronics, as in **biosensors** and **biochips**.

bioelement any element that is an essential component of living organisms. Bioelements include: as major elements, C, H, O, N, P, and S, found chiefly in combination in organic compounds, and the elements, Na, K, Mg, Ca, and Cl, found mainly as monatomic ions. Many other 'trace elements' occur in relatively minute amounts.

bioenergetics the study of energy transformations in living systems.

bioengineering 1 engineering relating to the operation on an industrial scale of biochemical processes, especially fermentation. This is usually now termed **biochemical engineering**. 2 the application of the physical sciences and engineering to the study of the functioning of the human body and to the treatment and correction of medical conditions.

biofuel cell any fuel cell (a cell in which electricity is produced directly by oxidation of fuel) in which one or both electrode reactions are promoted or catalysed by a biological process.

Bio-Gel *proprietary name for* a group of materials used in gel filtration, consisting of either cross-linked agarose (Bio-Gel A) or porous polyacrylamide (Bio-Gel P).

biogenesis 1 the synthesis of a substance in a living organism; biosynthesis. 2 the principle that a living organism can originate only from a parent or parents that are similar to itself. *Compare* **abiogenesis**. —**biogenetic**, **biogenetical**, **biogenous** *adj.*

biogenic produced by living organisms.

biogenic amine any of various amines, especially those with neurological activity, isolated from plants or animals.

bioinformatics *see* **Appendix E**.

biohazard any organism or material derived from a biological source that is hazardous to health or life.

bioinorganic chemistry a branch of inorganic chemistry concerned with the interactions between inorganic substances (especially metallic ions or their complexes) and biological or biochemical systems, and with the properties of related model systems. *Compare* **inorganic biochemistry**.

biolistics descriptive of the administration of DNA in gold particles, using a device known as a 'gun' to deliver the particles to the cell interior. One use has been in the development of vaccines by the administration of suitable genes to foreign cells.

biolith a rock or other deposit (e.g. peat, humus) formed from organic material.

biological *adj.* 1 of or pertaining to **biology**. 2 of or pertaining to life or living organisms. 3 a biological product that is used prophylactically or therapeutically. —**biologically** *adv.*

biological activity any activity of a substance that is demonstrable in living organisms. Biologically active substances are often of biological origin themselves.

biological clock any biological mechanism that allows the expression of a certain biological structure (e.g. a gene) or a biological function (e.g. sleep) at periodic intervals. The term is also used colloquially to describe ageing, e.g. in respect to a woman's ability to bear a child.

biologically active *or* **bioactive** active in a living organism.

biological value *abbr.*: B.V.; a measure of the value of a protein in a foodstuff for the maintenance of growth and normal functioning of any given animal or species. It is based on the amino-acid composition of the protein, its digestibility, and the availability of its digestion products.

biology 1 the scientific study of living organisms, including their structure, functioning, development, distribution, interrelationships, and evolution. 2 the animal and plant life of a particular region considered as a unit. 3 the structure, functioning, etc. of a particular organism or group of organisms. —**biologist** *n.*

bioluminescence the production of light by certain enzyme-catalysed reactions in living organisms. —**bioluminescent** *adj.*

biolysis any decomposition of organic material by biological means. —**biolytic** *adj.*

biomass 1 the total mass of living organisms, of a specified kind, forming a population inhabiting a given region. 2 the material produced by the growth of microorganisms, plants, or animals, especially as a product of or raw material for an industrial process, such as farming or fermentation.

biomedical science *or* **biomedicine** any branch of science that is relevant to medicine.

biomembrane any membrane surrounding a cell or a subcellular organelle, or derived from these structures.

biometry the statistical study of biology. —**biometric** *adj.*; **biometrically** *adv.*

biomimetic chemistry a branch of organic chemistry that aims to imitate natural reactions and enzymatic processes as a means to improve the power of organic chemistry.

biomolecular engineering a term sometimes used to cover those branches of biotechnology dealing with enzyme engineering and genetic engineering.

biomolecule any molecule, especially a macromolecule, that occurs in or is formed by living organisms. —**biomolecular** *adj.*

bioorganic chemistry a branch of organic chemistry concerned with the study of organic molecules from living systems.

biophotolysis any type of **photolysis** reaction occurring in a biological system; e.g. the lysis of a water molecule in the reactions of **photosystem II** during photosynthesis.

biophysical chemistry the application of the techniques or methods of physical chemistry to biological systems. It is principally concerned with the conformations, shape, structure, conformational changes, dynamics, and interactions of macromolecules and complexes or arrays of macromolecules. *Compare* **biophysics, physical chemistry**.

biophysics the application of physical techniques and physical methods of analysis to biological problems. Traditionally, the discipline has focused on two main areas: first, the transmission of nerve signals and the maintenance of electrical potentials across membranes; and second, large-molecule crystallography and enzyme structure and mechanisms. For the latter X-ray crystallography has been supplemented by a number of physical techniques, including nuclear magnetic resonance spectrometry, mass spectrometry, fluorescence-depolarization measurements, and circular-dichroism studies. —**biophysical** *adj.*; **biophysicist** *n.*

biopolymer any **polymer**, such as a protein, nucleic acid, or polysaccharide, occurring in, or formed by, living systems.

biopotency the extent to which a material (e.g. drug or hormone) influences a biological process.

bioproduct any (usually) useful product produced by living organisms or by systems derived from living organisms.

biopsy examination of (usually) a sample of tissue, cells, or fluid from a living human or animal for diagnostic purposes. The term is also now commonly used for the process of removing such a sample. *Compare* **necropsy**.

biopterin 2-amino-4-hydroxy-6-(1,2-dihydroxypropyl)-pteridine; 1-(2-amino-4-hydroxy-6-pteridinyl)-1,2-propanediol; a growth factor for certain protozoans, e.g. *Crithidia fasciculata* and *Trypanosoma platydactyli*. It is widely distributed in tissues and functions in a reduced form, **tetrahydrobiopterin**, as a hydroxylation coenzyme, e.g. in the conversion of phenylala-

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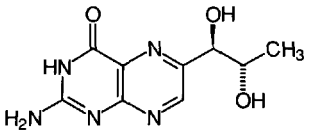
nine to tyrosine. It has been isolated from queen-bee jelly and is considered a growth factor for some insects.



bioreactor any reactor containing immobilized enzymes or cells that is used to effect specific chemical reactions in the production of some economically desirable product.

bioregulator omnibus term sometimes used for any substance occurring within a cell or organism that has a specific and reversible controlling action on a particular biochemical event within that cell or organism; it may be, e.g., a hormone, an enzyme, an intermediate metabolite, an inorganic ion, or a cyclic nucleotide.

bioremediation the use of biological systems to remedy environmental damage.

bios *the former name for* various growth factors required by yeast. Originally believed to be a single factor, it was later fractionated into bios I (shown to be **inositol**), bios IIA (**β-alanine**), and bios IIB (**biotin**).

bioscience(s) collectively all the individual branches of science that are concerned with biology.

biose disaccharide; stem name used in the established trivial names for particular disaccharides whether or not they contain a single type of sugar residue and linkage, as in cellobiose and gentiobiose.

+biose *suffix* used in nomenclature of glycolipids to indicate a compound containing an oligosaccharide moiety composed of two sugar residues (which may be the same or different), as in galabiose.

biosemiotics the study of signs, of communication, and of information in living organisms.

biosensor a device that uses specific biochemical reactions mediated by isolated enzymes, immunosystems, tissues, organelles, or whole cells to detect chemical compounds, usually by electrical, thermal, or optical signals.

biospecific describing: **1** a reagent, e.g. an antibody or hormone, that can recognize and interact only with cells (e.g. within a mixed population of cells) displaying a particular surface characteristic, e.g. a corresponding antigen or receptor. **2** any reagent that, in a similar way, recognizes and interacts with a particular biospecifically occurring substance. **3** any reagent that interacts specifically with a particular biomolecule (e.g. an enzyme). **4** the reaction between two biospecific reagents.

biospecific-elution chromatography *an alternative name for* **affinity-elution chromatography** (when the ligand in the eluting solvent is a biospecific macromolecule).

biosphere the parts of the Earth's crust and atmosphere that contain living organisms.

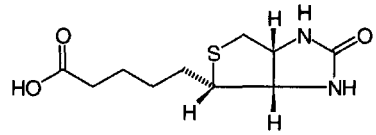
biosynthesis the production of substances by processes occurring in living systems; **anabolism**; **biogenesis**. *Compare* **biodegradation**.

biosynthetic **1** of or relating to **biosynthesis**. **2** any substance produced by biosynthesis.

biosynthetic pathway any metabolic pathway effecting **biosynthesis**; an anabolic pathway.

biotechnology 'the integration of natural sciences and engineering sciences in order to achieve the application of organisms, cells, parts thereof and molecular analogues for products and services' (European Federation of Biotechnology General Assembly, 1989); a field of technological activity in which biochemical, genetic, microbiological, and engineering techniques are combined for the pursuit of technical and applied aspects of research into biological materials and, in particular, into biological processing. It includes traditional technologies such as fermentation processes, antibiotic production, and sewage treatment, as well as newer ones such as **biomolecular engineering**, and **single-cell protein** production. —**biotechnological** *adj.*

biotin *cis*-tetrahydro-2-oxothieno[3,4-*d*]imidazoline-4-valeric acid; hexahydro-2-oxo-1*H*-thieno[3,4-*d*]imidazole-4-pentanoic acid; vitamin H; *formerly known as* bios IIB and coenzyme RCO_2; a substance the (+) enantiomer of which is very widely distributed in cells and serves as a carrier in a number of enzymic β-carboxylation reactions. In biotin-containing enzymes the biotin is covalently bound at the active site through an amide link to the ε-amino group of a lysine residue. It was first found as a growth factor for yeasts. *Compare* **biocytin**. *See also* **streptavidin**.



biotin carboxylase *see* **acetyl-CoA carboxylase**.

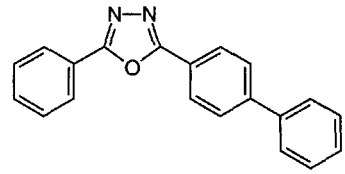
biotinyl the acyl group derived from **biotin**.

biotinylation the act or process of attaching a biotinyl residue by use of an appropriate reactive derivative, e.g. biotin 4-nitrophenyl ester. It is useful for labelling cell-surface functional groups or biologically active molecules. The presence of the label is subsequently detected, or the labelled material is separated, by means of the specific and high-affinity avidin–biotin reaction, using avidin or **streptavidin** conjugated with, e.g., a fluorochrome, an enzyme, an antibody, or an immobilizing agent. —**biotinylate** *vb.*; **biotinylated** *adj.*

biotransformation the conversion or conjugation of a foreign compound introduced into an organism or a culture of cells, especially (*in biotechnology*) with formation of a substance of commercial value. *Compare* **detoxication**.

BiP *abbr. for* binding protein.

biphenylylphenyloxadiazole *abbr.*: PBD; 2-phenyl-5-(4-biphenylyl)-1,3,4-oxadiazole; a high-efficiency primary scintillator. The *tert*-butyl derivative, 2-(4-*tert*-butylphenyl)-5-(4-biphenylyl)-1,3,4-oxadiazole (*abbr.*: butyl-PBD) has greater solubility and only a slightly lower photon yield. *See also* **scintillation cocktail**.



biphosphate *an obsolete name for* the anion $H_2PO_4^-$ or $PO_2(OH)_2^-$, now correctly termed dihydrogenphosphate.

biradical *or* **diradical** any molecular entity in an electronic state (described by a formula or by a combination of contributing structures) that contains two unpaired electrons in atomic orbitals on different atoms (*compare* **carbene**). Both singlet and triplet species are embraced.

birefringence *an alternative term for* **double refraction**. —**birefringent** *adj.*

bis+ *comb. form* **1** denoting two, twice, doubled; *see also* **bi+** (def. 1), **di+** (def. 1). **2** *(in chemical nomenclature)* **a** indicating the presence in a molecule of two identical organic groups each substituted in the same way, e.g. **bis(2-chloroethyl)sulfide**. **b** indicating the presence in a molecule of two separate inorganic oxoacid residues, e.g. fructose 1,6-bisphosphate (formerly known as fructose 1,6-diphosphate). *Compare* **di+** (def. 1).

bisalbuminemia *or (esp. Brit.)* **bisalbuminaemia** a symptom-

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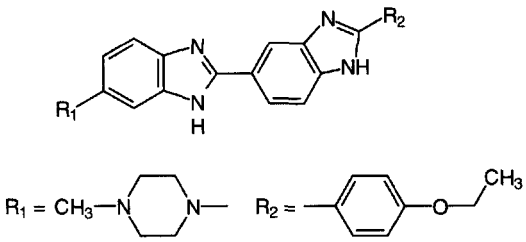
less human condition in which the presence of a variant serum albumin leads to a double albumin band on electrophoresis of serum proteins.

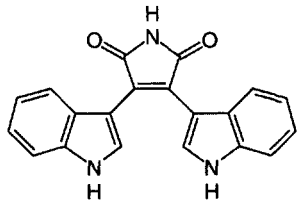
bisbenzimide 4-{[5-(4-methyl-1-piperazinyl)-2-benzimidazolyl]-2-benzimidazolyl} phenol (Hoechst 33258) or its ethyl ether (Hoechst 33342); a substance that is useful as a DNA-binding fluorochrome for staining chromosomes within cell nuclei. It is believed to be specific for A–T base pairs.



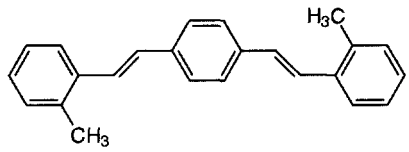
bis(2-chloroethyl)sulfide *or (formerly)* **mustard gas** ($ClCH_2$–$CH_2)_2S$; a bifunctional alkylating agent that causes lethal cross-linking of DNA chains.

Bishop, John Michael (1936–), US microbiologist; Nobel Laureate in Physiology or Medicine (1989) jointly with H. E. Varmus 'for their discovery of the cellular origin of retroviral oncogenes'.

bisindolylmaleimide GF 109203X; a protein kinase inhibitor, structurally similar to **staurosporine**, that is highly selective for **protein kinase C** (PKC), though not between isotypes α, βI, βII, or γ. It acts as a competitive inhibitor at the ATP-binding site on PKC. It exhibits a K_i of 14 nM for the purified enzyme, but its potency on whole cells is much lower (K_i 1–2 μM), possibly owing to high cellular ATP levels.



bismethylstyrylbenzene *abbr.*: bis-MSB; 1,4-bis(2-methylstyryl)-benzene; a secondary scintillator with good resistance to quenching and low reactivity with compounds in samples. *See also* **scintillation cocktail**.

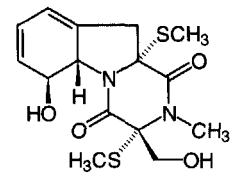


bis(methylthio)gliotoxin a naturally occurring analogue of **gliotoxin**. It inhibits platelet activating factor (PAF)-induced platelet aggregation (IC_{50} = 84 μM) (but not platelet aggregation induced by arachidonic acid or ADP) and *in vivo* PAF-induced bronchoconstriction; it lacks the antiviral and immunomodulating effect of gliotoxin. (Illustrated top right.)

bis-MSB *abbr. for* bismethylstyrylbenzene.

bisphosphate any compound containing two independent phosphoric residues in ester linkages, at positions indicated by locants. *Compare* **diphosphate** (def. 3, 4).

bisphospho+ *prefix* to a chemical name indicating the presence of two independent phosphoric residues in ester linkages, at positions indicated by locants. *Compare* **diphospho+**.



bis(methylthio)gliotoxin

2,3-bis(phospho)-D-glycerate *a recommended name for* (*R*)-[2,3-dihydroxypropanoate 2,3-bis(dihydrogenphosphate)] (formerly termed 2,3-diphosphoglycerate); *abbr.*: BPG; it decreases the dioxygen affinity of hemoglobin, its concentration in the erythrocyte being regulated by **bisphosphoglycerate mutase** (synthesis) and **bisphosphoglycerate phosphatase** (degradation). It does not pass through the erythrocyte membrane. *See also* **bisphosphoglycerate pocket**.

bisphosphoglycerate mutase *abbr.*: BPGM; EC 5.4.2.4; *systematic name*: 3-phospho-D-glycerate 1,2-phosphomutase; *other names*: 2,3-bisphosphoglycerate mutase; 2,3-bisphosphoglycerate synthase; diphosphoglycerate mutase; glycerate phosphomutase; bisphosphoglycerate synthase. An enzyme that catalyses the reaction:

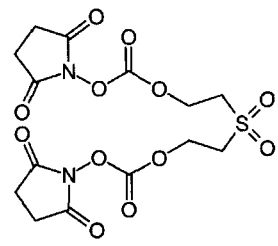
3-phospho-D-glyceroyl phosphate = 2,3-bisphospho-D-glycerate.

The enzyme plays a major role in regulating the dioxygen affinity of hemoglobin by controlling 2,3-bisphosphoglycerate concentration in the erythrocyte, but with a reduced activity. Example from human: database code PGME_HUMAN, 258 amino acids (29.84 kDa).

bisphosphoglycerate phosphatase EC 3.1.3.13; *systematic name*: 2,3-bisphospho-D-glycerate 2-phosphohydrolase; an enzyme that catalyses the hydrolysis of 2,3-bisphosphoglycerate to 3-phosphoglycerate and orthophosphate; it thereby assists regulation of the concentration of 2,3-bisphosphoglycerate.

bisphosphoglycerate pocket *abbr.*: BPG pocket; the cavity (pocket) between the two β chains of deoxyhemoglobin in which a single molecule of 2,3-bisphospho-D-glycerate (BPG) binds; the binding of this molecule reduces the affinity of hemoglobin for dioxygen. Residues Val^1 (terminal $-NH_3^+$), His^2, Lys^{82}, and His^{143} of each β chain participate in this binding. It plays an important part in establishing the difference in oxygen affinity that is found between maternal and fetal hemoglobin; in fetal hemoglobin, the γ chain has a serine in the position occupied by His^{143} of the β chain of the adult hemoglobin, which weakens the affinity of fetal hemoglobin for BPG and thus results in a higher affinity for dioxygen than adult hemoglobin.

bis[2-succinimidooxycarbonyloxyethyl]sulfone a non cytotoxic, homobifunctional, lysine-specific cross-linking agent that reacts at 0 °C; the cross-links can be reversed at pH 11.6 at 37 °C.



2,5-bis(3,4,5-trimethoxyphenyl)-1,3-dioxolane a substance, the *trans*-isomer of which inhibits platelet activating factor-induced platelet aggregation. The *cis*-isomer is inactive.

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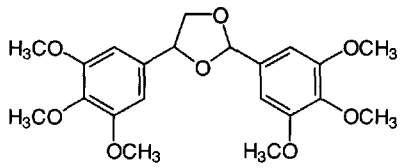
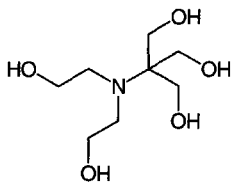
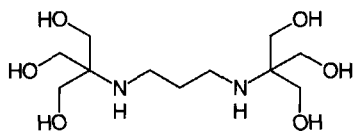


2,5-bis(3,4,5-trimethoxyphenyl)-1,3-dioxolane

Bistris *or* **bis-tris** *abbr. for* bis(2-hydroxyethyl)imino-tris-(hydroxymethyl)methane; 2-[bis(2-hydroxyethyl)amino]-2-(hydroxymethyl)-propane-1,3-diol. A buffer substance useful for the calibration of glass electrodes and for the preparation of biochemical and biological buffer solutions; pK_a (25 °C) = 6.5. It is inexpensive, stable, and readily crystallizable.



bis-tris propane *abbr. for* 1,3-bis[tris(hydroxymethyl)methylamino]propane; a water-soluble buffer substance used for the preparation of biochemical and biological buffer solutions; pK_a (20 °C) = 6.8.



bit a single binary digit having the value of either 0 or 1; the smallest unit of information in a binary system. A group of (usually) eight bits comprises a **byte**, which can represent numbers between 0 and 11111111 in binary (equal to 0 and 255 in decimal). [*abbr. for* binary digit.]

bithorax complex *see* **BX-C**.

Bittner factor *or* **Bittner particle** *former name for* murine mammary tumour virus. [After John Joseph Bittner (1904–61), US biologist.]

biuret reaction the formation of a characteristic purple colour when biuret (carbamoylurea) or compounds containing two or more adjacent peptide bonds (e.g. proteins) react with copper sulfate in alkaline solution. It forms the basis of the **biuret test**, a colorimetric method for the qualitative or quantitative determination of proteins.

Bjerrum formation function a function used in studies of the binding of n ligand atoms, ions, or molecules to an acceptor atom, ion, or molecule. It is:

$$\nu = (K_1[L] + 2K_1K_2[L]^2 + \ldots nK_1K_2\ldots K_n[L]^n)/(1 + K_1[L] + 2K_1K_2[L^2] + \ldots nK_1K_2\ldots K_n[L]^n),$$

where ν is the average number of ligand molecules bound per molecule of acceptor; K_1, K_2, ...K_n are the stepwise formation (stability) constants of the n complexes; and $[L]$ is the free ligand concentration. This function expresses an unambiguous connection between the quantity ν and $[L]$. It is a generalized form of the **Adair equation**. [After Jannik Bjerrum (1909–), Danish chemist who described it in 1941.]

Bjerrum plot a plot of ν, the average number of ligand molecules bound per molecule of acceptor, versus $-\log[L]$, where $[L]$ is the free ligand concentration. It is used for evaluating the association constants in a **Bjerrum formation function**.

Bk *symbol for* berkelium.

BK *abbr. for* bradykinin.

BK_{1-8} *abbr. for* des-Arg^9-bradykinin (*see* **bradykinin**).

bla *symbol for* β-lactamase gene.

Black, (Sir) James Whyte (1924–), British pharmacologist distinguished for his discoveries of blockade of β-adrenoceptors and of H_2-receptors by novel drugs; Nobel Laureate in Physiology or Medicine (1988) jointly with G. B. Elion and G. H. Hitchings 'for their discoveries of important principles for drug treatment'.

black lipid membrane *abbr.*: BLM; *other names*: black lipid film; bimolecular lipid membrane; bilayer lipid membrane; lipid bilayer. An experimental membrane formed by introducing a small amount of suitable lipid solution on to an opening in the wall of a hydrophobic support immersed in an aqueous solution. The thickness of the black membrane does not differ greatly from the length of two of the lipid molecules used and is often about 4.5 nm.

blank (determination) any analytical mixture from which analyte is deliberately omitted and which undergoes the same procedures as the complete mixture. It is used to ascertain the contribution of extraneous factors, e.g. reagent impurities or photometric absorption by the reagents, to the analytical result.

blast+ *a variant form of* **blasto+**.

+blast *suffix* denoting a formative cell, e.g. erythroblast, fibroblast, osteoblast.

blast cell *or* **blastocyte** any undifferentiated embryonic cell. Such cells characteristically have a cytoplasm rich in RNA, and are actively synthesizing DNA.

blast crisis the appearance of heterogeneity in the cell surface characteristics of white blood cells when chronic myeloid leukemia evolves into acute leukemia. This process is virtually inevitable and often rapid.

blasto+ *or (before a vowel)* **blast+** *prefix* denoting **1** an embryo in its early stages; e.g. blastocyst, blastula. **2** a germ cell; e.g. blastocyte.

blastokinin *see* **uteroglobin**.

blast transformation *see* **transformation** (def. 3).

bleb **1** a spherical vesicle, about 10 μm in diameter, formed when a chloroplast swells on suspension in very hypotonic medium. It is bounded by a single membrane, on the surface of which a part of the **thylakoid** system remains concentrated in a few patches. **2** animal membranes are said to form blebs under special conditions that cause small vesicles to pinch off.

blender *or (sometimes, US)* **blendor** a device for disrupting tissue or any aggregate. It consists of blades rotating at the bottom of a glass or stainless-steel vessel (originally named a **Waring blendor**, from a trade name); in an alternative design, known as a top-drive blender, the blades rotate on a spindle from the top of the vessel. The method is undiscriminating and may damage organelle membranes through excessive force or generation of heat. For more precise work, a **Potter–Elvehjem homogenizer** or a **Dounce homogenizer** preserves organelle structure.

bleomycin any of a group of related glycopeptide antibiotics isolated from *Streptomyces verticillus*. Bleomycin acts to stop the cell cycle in the G_2 phase (*see* **cell-division cycle**). It is used to induce synchrony in cell cultures and as an antineoplastic agent, especially in lymphomas.

blepharoplast *an alternative term for* **basal body** of a flagellate.

Blk a gene encoding a protein tyrosine kinase of the Src family, specifically expressed in the B-cell lineage.

BLM *abbr. for* black lipid membrane.

Bloch 1 Felix Bloch (1905–83), Swiss-born US physicist notable for his extensive studies in solid-state physics, for his measurement (with L. W. Alvarez) of the magnetic moment of the neutron, and for his discovery (independently of E. M. Purcell) of

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the phenomenon of **nuclear magnetic resonance** of certain atomic nuclei; Nobel Laureate in Physics (1952) jointly with E. M. Purcell 'for their development of new methods for nuclear magnetic precision measurements and discoveries in connection therewith'. **2 Konrad Emil Bloch** (1912–), German-born US biochemist distinguished for his extensive studies by isotope techniques of the biosynthesis of cholesterol, creatine, and protoporphyrin; Nobel Laureate in Physiology or Medicine (1964) jointly with F. Lynen 'for their discoveries concerning the mechanism and regulation of the cholesterol and fatty acid metabolism'.

block **1** *(in chemistry)* a portion of a polymer molecule comprising many **constitutional base units**; such a portion has a constitutional or configurational feature not present in the adjacent multiple-unit portions. **2** *(in physiology)* an interference in the normal metabolic or physiological functioning of an organ or tissue; e.g. metabolic block, heart block. **3** to impede, retard, or prevent an action or activity, e.g. of an agonist, antigen, chemical reagent, enzyme, or receptor.

blockade **1** *(in pharmacology)* the saturation of a specific type of receptor with an antagonist to its normal agonist. **2** *(in immunology)* the overloading or saturation of the **reticuloendothelial system** with inert particles, such as carbon particles. **3** to impose any such blockade.

blocker something that blocks an action or activity; an antagonist or inhibitor.

blocking agent **1** a chemical reagent that introduces a **blocking group**. **2** a specific pharmacological antagonist.

blocking antibody **1** an incomplete antibody that does not agglutinate its antigen but attaches to it and so prevents its agglutination by normal, complete antibody. **2** antibody formed during specific **desensitization** in **atopy**.

blocking group **1** *or* **protecting group** a chemical group, often easily removable, that is substituted into a reactive part of a molecule to prevent its participation in subsequent chemical or enzymic reactions occurring at another part of the molecule. **2** a chemical group, not easily removable, that is substituted into the active site of an enzyme to prevent its action.

block polymer a polymer whose molecules contain two or more species of **block** (def. 1) attached linearly.

blood a fluid tissue in animals that acts primarily as a transport medium. It is contained in vessels or spaces lined with endothelial cells. Metabolites, nutrients, and excretory substances are carried in solution or suspension from one part of the body to another. Respiratory pigments are often present to assist in the transport of dioxygen. It may also contain suspended cells.

blood–brain barrier the semipermeable membranous barrier that regulates the passage of dissolved materials from the blood into the cerebrospinal fluid that bathes the brain and spinal cord.

blood coagulation *or* **blood clotting** a mechanism that prevents blood loss at the site of an injury. It involves the formation of a semisolid mass of material, the blood clot, which plugs the wound. The clot consists of aggregated platelets and a mesh of fibrin molecules. The fibrin components include 13 or 14 plasma proteins, at least one tissue protein, phospholipid membrane surfaces, Ca^{2+} ions, and platelets. The current concept of the mechanism has changed from one involving a linear sequence of activations of proenzymes to one involving protein–protein and protein–lipid–Ca^{2+} interactions between proteinase, protein substrates, and protein cofactors to give discrete complexes and reaction steps. The following factors are involved in coagulation:

Factor I (*or* **fibrinogen**) concn. ≈2–4 g L^{-1} human plasma; a soluble fibrous protein of 330 kDa, it has an axial ratio of ≈5 and is made up of six disulfide-linked polypeptide chains; two Aα chains (66 kDa); two Bβ chains (52 kDa); and two γ chains (47 kDa). After proteolysis by thrombin it polymerizes to form an insoluble fibrin clot.

Factor II (*or* **prothrombin**) concn. 200 mg L^{-1} human plasma, 72.5 kDa; a vitamin K-dependent single-polypeptide-chain glycoprotein containing ten γ-carboxyglutamate residues. It is converted to **thrombin** (*or* fibrinogenase), EC 3.4.21.5, by the proteinase factor Xa.

Factor III (*or* thromboplastin *or* tissue factor) a factor that, when added to blood plasma, markedly shortens the time required for clot formation. Example from human (precursor): database code TF_HUMAN, 295 amino acids (33.07 kDa).

Factor IV (*or* calcium ion) calcium ions form bridges between vitamin K-dependent proteins and acid phospholipids of cell membranes. They also stabilize factor V and fibrinogen, and are involved in activation of factor XIII.

Factor V (*or* accelerator globulin *or* proaccelerin) a glycoprotein of ≈330 kDa. After activation to **factor Va** (accelerin) it acts with the proteinase factor Xa in activating prothrombin. Example from human (precursor): database code FA5_HUMAN, 2224 amino acids (251.70 kDa).

Factor VI an obsolete term (originally named accelerin).

Factor VII (*or* proconvertin) concn. 2 mg L^{-1} human plasma; 50 kDa; a vitamin K-dependent single-polypeptide-chain glycoprotein containing γ-carboxyglutamate residues. It is the precursor of **factor VIIa**, convertin, a Ca^{2+}-dependent proteinase, EC 3.4.21.21, that activates factor X and is the first component of the extrinsic pathway of coagulation. Example from rabbit (precursor): database code FA7_RABIT, 443 amino acids (48.85 kDa).

Factor VIII (*or* antihemophilic factor); an accessory protein that participates with proteinase factor IXa in the activation of factor X in the intrinsic pathway of coagulation. Example from mouse (precursor): database code FA8_MOUSE, 2319 amino acids (266.15 kDa).

Factor IX (*or* Christmas factor) concn. 3–4 mg L^{-1} human plasma; 57 kDa (human), 55.4 kDa (bovine); a vitamin K-dependent single-polypeptide-chain glycoprotein containing 17% carbohydrate (human; 25% in bovine) and γ-carboxyglutamate residues. After proteolytic activation it consists of two chains: **factor IXa**, a serine proteinase, EC 3.4.21.22, of 27 kDa that activates factor X in the intrinsic pathway of coagulation; and a light chain of 16 kDa that contains the γ-carboxyglutamate residues. Example from dog (precursor): database code FA9_CANFA, 452 amino acids (50.83 kDa).

Factor X (*or* Stuart–Prower factor; *other names*: Stuart factor; thrombokinase; prothrombase; prothrombinase) concn. 6–8 mg L^{-1} human plasma; a vitamin K-dependent two-polypeptide-chain glycoprotein, containing 15% carbohydrate (human; 10% in bovine). The 40 kDa chain is a serine proteinase while the 15 kDa chain contains 12 γ-carboxyglutamate residues. Example (precursor) from human: database code FA10_HUMAN, 488 amino-acid residues (54.67 kDa). It is the circulating precursor to the proteinase **factor Xa**, EC 3.4.21.6, that converts prothrombin into thrombin by selective cleavage of Arg-|-Thr then Arg-|-Ile bonds.

Factor XI (*or* plasma thromboplastin antecedent) 160 kDa (human), 124 kDa (bovine); a protein of two disulfide-linked chains of apparently equal molecular mass. Example from human: database code FA11_HUMAN, 625 amino acids (70.03 kDa). It is the circulating precursor of the serine proteinase **factor XIa**, EC 3.4.21.27, to which it is converted by proteolysis: selective cleavage of Arg-|-Ala and Arg-|-Val bonds in factor IX to form factor IXa triggers the middle phase of the intrinsic pathway of blood coagulation by activating factor IX. Factor XIa converts factor IX into factor IXa.

Factor XII (*or* Hageman factor) 80 kDa (human), 74 kDa (bovine); a single-polypeptide-chain glycoprotein. It is the circulating precursor of the proteinase **factor XIIa**, which activates factor XI. Example from human (precursor): database code FA12_HUMAN, 615 amino acids (67.82 kDa).

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Factor XIII (*or* plasma transglutaminase) 320 kDa (plasma, tetrameric), 160 kDa (platelets, dimeric). An enzyme precursor whose subunits are proteolytically cleaved by thrombin to form the transglutaminase, **factor XIIIa**, EC 2.3.2.13, which covalently cross-links fibrin monomers into the fibrin polymer.

Prekallikrein a plasma protein, 88 kDa (bovine), that is the precursor of the proteinase **kallikrein**. This consists of a heavy chain (52 kDa) and a light chain (33–38 kDa) and cleaves factor XII to form factor XIIa.

High-molecular-weight kininogen a single-polypeptide-chain glycoprotein of ≈150 kDa (human), 76 kDa (bovine). It is the source of **bradykinin**, which is released from it by **kallikrein**, and acts as an accessory protein in the activation of factor XI by factor XIIa. Example from *Bos taurus* (precursor): database code KNH1_BOVIN, 621 amino acids (68.89 kDa).

Plasminogen 86 kDa (human); a single-polypeptide-chain protein that, on proteolysis, is converted into the protease **plasmin**, which degrades the fibrin clot.

There are two pathways of coagulation: in the **intrinsic pathway**, which occurs during the clotting of platelet-poor plasma, activation of factor X to factor Xa is effected by the combination of factor IXa + factor VIIIa + Ca^{2+} + phospholipid; in the **extrinsic pathway** the earlier stages of the cascade are bypassed and the activation of factor X to factor Xa is effected by the combination of factor VIIa + thromboplastin; this second pathway occurs when tissue extracts are present in optimal amounts and is much more rapid than the intrinsic pathway.

blood group any of various systems of classifying erythrocytes according to their surface isoantigens. In humans 14 different, genetically independent blood-group systems are known. They arise from naturally occurring antibodies and from the **blood-group substances**, antigenic substances present on the surface of the erythrocytes of only certain members of a species. These antigens are also found in a wide variety of other tissues, including endothelial and epithelial cells, and in certain body fluids. The specificities of the blood-group antigens arise in some cases from oligosaccharide chains linked to protein or lipid (ceramide); antigens that fall into this category are those associated with the ABH system, Lewis system, Ii system, and P1/P-related system. In other cases, antigenicity arises directly from the polypeptide chain composition of a surface protein; antigens that fall into this category are associated with the MN system, Ss system, Gerbich system, Rhesus system, Kell system, Duffy system, and Cromer-related system. The blood-group substances were discovered because of the presence in human blood of naturally occurring antibodies (i.e. not resulting from infection or other external cause) that react with these antigens on red blood cells causing them to agglutinate. Only the presence of a blood-group antigen during fetal life ensures that no antibody against it will be produced. Hence if blood from an individual (the donor) who lacks a particular antigen is transfused into an individual (the recipient) who possesses the same antigen, a transfusion reaction will result in the recipient owing to the presence in the donor's blood of antibody against the antigen in question. The blood-group substances have therefore been of interest largely in relation to blood transfusion, and in most cases the true physiological function of these substances is unknown.

blood-group substance any of numerous antigenic substances present on the surface of erythrocytes of certain members of a species but absent from those of other members of the same species. These same antigens are also found in a wide variety of tissues and in certain body fluids, e.g. saliva, milk, gastric juice, seminal fluid, urine, and ovarian-cyst fluid. The specificities of the A, B, and H antigens of the **ABO system** are determined by structures present at the nonreducing ends of oligosaccharides of both glycoproteins and glycolipids. The **Lewis antigens**, Le_a and Le_b, are associated with glycosphingolipids adsorbed from plasma lipoproteins on to adult cells and are not synthesized in the developing erythrocyte. Antigenic determinants of the **MN system** are associated with glycoproteins rich in sialic acid.

blood plasma 1 the fluid portion of blood in which the red blood cells and other cellular components (the 'formed elements') are suspended. Clotting may be prevented by the addition of disodium hydrogen citrate which removes ionized Ca^{2+} by the formation of an un-ionized complex. Fluoride or oxalate may also be used to precipitate the Ca as an insoluble salt. **Heparin** is often used. When whole blood containing such an anticoagulant is centrifuged, the formed elements sediment in a volume equal to about 45% of the total volume of blood. The supernatant is known as the plasma. In vertebrates it is clear and almost colourless and clots as easily as whole blood. *See also* **anticoagulant**. *Compare* **serum**.

blood sugar *old term for* the glucose concentration in the blood; when estimated by older methods it included small amounts of other reducing substances. *See also* **glycemia**.

blotting *or* **blot transfer** a technique useful for identifying similar macromolecules, e.g. sets of DNA or RNA fragments, or mixtures of intact proteins, that are separable by gel electrophoresis. The separated components are then transferred from the gel to a sheet of an appropriate medium while preserving their two-dimensional relationships. This can be achieved either by capillary flow between an underlying wick loaded with buffer solution and an overlay of dry blotting paper, or by applying an electric potential to move separated components on to the medium, to which they bind firmly. Once on the transfer medium the substances may be detected with specific radioactive or fluorescent probes, e.g. complementary polynucleotides or antibodies. The original version of the technique, used for DNA fragments and often referred to as **Southern blotting**, has been extensively developed and adapted for other applications, e.g. **dot hybridization** (or dot blotting), **colony hybridization**, **electrophoretic transfer**, **Northern blotting**, and **Western blotting**.

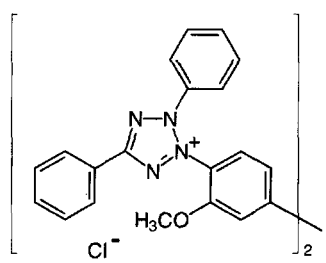
blue agarose any insoluble beaded form of agarose gel that is artificially cross-linked between the individual polysaccharide chains and conjugated with the dye Reactive Blue 2. Carboxymethyl (CM) or diethylaminoethyl (DEAE) groups may also have been introduced. It is useful in **triazine-dye affinity chromatography**.

blue dextran a soluble dextran, of average M_r 10^6, conjugated with the dye Reactive Blue 2. It is useful in gel filtration for checking column packing and determining the void volume.

blue-green algae *an alternative name for* **cyanobacteria**.

blue oxidase any of a small number of copper-containing oxidase enzymes in which the product of enzyme action in the reduction of dioxygen is water. Blue oxidases are the most complicated of copper proteins; the blue colour is due to a strong absorption band around 600 nm. Among the blue oxidases are laccase (EC 1.10.3.2), L-ascorbate oxidase (EC 1.10.3.3), and the weak oxidase **ceruloplasmin**.

blue shift any shift of the peaks of absorption or emission of a spectrum of electromagnetic radiation to shorter wavelengths, including from the visible to the ultraviolet region.



Blue Tetrazolium

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Blue Tetrazolium *or* **Tetrazolium Blue** 3,3′-dianisole bis[4,4′-(3,5-diphenyl)tetrazolium chloride]; a dye that yields a dark-blue diformazan pigment on reduction; it has a redox potential of approximately –0.08 V. It is useful as a stain for bacteria and moulds, in histochemical studies to demonstrate oxidoreductase activity, and in the colorimetric assay of some dehydrogenases.

blunt end (of DNA) *an alternative term for* **flush end** (of DNA).

B lymphocyte *or* **B cell** *or (archaic)* **bursacyte** any 'bursa-dependent' lymphocyte concerned in the synthesis of circulating antibody. B lymphocytes arise from primitive lymphoid cells of the bone marrow and develop into the **plasma cell** series. Their maturation is determined by processing within the **bursa of Fabricius** in birds, or equivalent hematopoietic tissue in other vertebrates. B lymphocytes may be differentiated from **T lymphocytes** by their surface markers which contain immunoglobulins. In humans the majority of B lymphocytes are derived from bone marrow stem cells, but a minor population, distinguished by the CD5 marker, appears to form a self-renewing set. Cells in this set respond to a number of common microbial antigens and sometimes generate **autoantibodies**.

Bmi-1 a murine gene encoding a protein that is probably a transcriptional regulator. It is named from B-cell-specific Moloney murine leukemia virus integration site. The protein contains putative **zinc finger** and **helix-loop-helix** domains, as well as C-terminal PEST sequences. *See* **PEST hypothesis**.

BMP *abbr. for* bone morphogenetic protein.

BMR *abbr. for* basal metabolic rate.

BNP *abbr. for* brain natriuretic peptide (*see* **natriuretic peptide**).

boat conformation any conformation of a nonplanar six-membered saturated ring compound when ring atoms in relative positions 1, 2, 4, and 5 lie in one plane, and those in relative positions 3 and 6 lie on the same side of that plane. Boat conformations of a monosaccharide or monosaccharide derivative may be designated by the conformational descriptor *-B*. *See also* cyclic compounds at **conformation**.

Boc *or* ***t*-BOC** *symbol for* the *tert*-butoxycarbonyl group, $(CH_3)_3C–O–CO–$, a **protecting group** used in polypeptide chemistry. It can be introduced using reagents such as di-*tert*-butyl dicarbonate (Boc anhydride).

BOD *abbr. for* biochemical oxygen demand.

body water the water content of the body of an organism. The **total body water** (*abbr.* TBW) of a man of average build (70 kg) has a volume of approximately 42 L and represents ≈ 60% of the body weight. It may be divided functionally into two parts: **intracellular fluid** and **extracellular fluid**.

Bohr **1 Christian Bohr** (1855–1911), father of N. H. D. Bohr (*see* def. 2), Danish physiologist noted for his researches on the binding of dioxygen to hemoglobin (*see* **Bohr coefficient**, **Bohr effect**). **2 Niels Henrik David Bohr** (1885–1962), son of C. Bohr (*see* def.1), Danish physicist distinguished for his theories of atomic and nuclear structure and their applications; Nobel Laureate in Physics (1922) 'for his services in the investigation of the structure of atoms and of the radiation emanating from them'.

Bohr coefficient (for hemoglobin) the ratio of the change in the logarithm of the partial pressure of oxygen when there is half-saturation of the hemoglobin to the change in pH; i.e. $\Delta\log P_{50}/\Delta pH$. *See also* **Bohr effect**. [After C. Bohr; *see* **Bohr** (def.2).]

Bohr effect the variation of oxygen affinity of hemoglobin with pH (the oxygen affinity increases with increasing pH). It is one of the effects arising from oxygen-linked acid groups in hemoglobin and similar oxygen-carrying proteins, and also encompasses similar effects involving other acid-linked functions, e.g. oxidation loss of protons causing increased dioxygen binding. The effect was discovered by C. Bohr *et al.* following observations that changes in the partial pressure of CO_2 influence the oxygen equilibrium of the blood.

Bohr magneton *symbol*: μ_B; the intrinsic magnetic moment of an electron given by $\mu_B = eh/4\pi m_e$, where e is the elementary charge, h is the Planck constant, and m_e is the rest mass of an electron. It is a fundamental physical constant, of value $9.274\ 015\ 4(31) \times 10^{-24}$ J T^{-1}. *Compare* **nuclear magneton**. [After N. H. D. Bohr; *see* **Bohr** (def. 2).]

boivinose the D-enantiomer, 2,6-dideoxy-D-*xylo*-hexose, is a component of some **cardiac glycosides**.

Bollum's enzyme DNA nucleotidylexotransferase, EC 2.7.7.31. *See* **terminal transferase**. [After Frederick James Bollum (1927–), who described it in 1971.]

Bolton and Hunter reagent *or* **Bolton–Hunter reagent** 3-(4-hydroxyphenyl) propionic acid *N*-hydroxysuccinamide ester, iodinated with ^{125}I. This may be the di-iodo derivative, or the commercially available mono-iodo *N*-succinimidyl 3-(4-hydroxy-5-[^{125}I]iodophenyl)propionate; a reagent for **conjugation labelling** of polypeptides or proteins with iodine-125. It is specific for free amino groups, which under mild conditions become acylated to form (4-hydroxy-5-[^{125}I]iodophenyl)propionylamino groups. [After Anthony E. Bolton and William M. Hunter who described its use in 1972.]

Boltzmann constant *symbol*: k; the ratio of the gas constant, R, to the Avogadro constant, N_A. It is given by $k = R/N_A = 1.380\ 658\ (12) \times 10^{-23}$ J K^{-1}. [After Ludwig Boltzmann (1844–1906), Austrian physicist.]

Boltzmann distribution law a law describing the population distribution of a system of particles in different energy states but at thermal equilibrium, given by: $n_i/n_0 = e^{-(E_i - E_0)/kT}$, where n_i is the number of particles in energy state i, n_0 is the number in the lowest energy state, E_i and E_0 are the energies of states of i and 0 respectively, T is the thermodynamic temperature, and k is the **Boltzmann constant**.

bolus **1** a soft, rounded mass, especially of chewed food. **2** a large pill, as used in veterinary or clinical medicine.

bomb calorimeter an apparatus with which the heat of combustion of a substance may be determined. The substance is placed in a metal bomb with dioxygen under pressure, and then ignited electrically. The heat evolved is measured by the rise in temperature of the water in a surrounding jacket.

bombesin a tetradecapeptide amide isolated from frog skin. It has an N-terminal 5-oxoprolyl residue and shows striking sequence homology with other peptides isolated from amphibian skin, all of which have a C-terminal methioninamide residue. The sequence is (toad):

XQRLGNQWAVGHLM–NH_2,

database code (for precursor) BOMB_BOMOR, 119 amino acids (13.86 kDa). In mammals it is a potent releaser of, *inter alia*, gastrin and cholecystokinin, and bombesin-like immunoreactivity has been detected in mammalian gut and brain. It is mitogenic in a number of cell types and stimulates smooth muscle contraction. The peptide is said to occur in gastrointestinal nerves of mammals, while in frogs and birds it occurs in endocrine cells.

bombesin receptor any of several membrane proteins that bind bombesin and mediate its intracellular effects. Binding studies have indicated two receptor subtypes: on gastrin releasing peptide (GRP)-preferring receptors (e.g. rat pancreas), GRP is more potent than neuromedin B; on other receptors (e.g. rat esophagus) neuromedin B is more potent than GRP. All receptors are of the seven-transmembrane-helix, G-protein-coupled type. The effector pathway involves the phosphoinositide/Ca^{2+} second messenger system (*see* **phosphatidylinositol cycle**). Example from human: database code BRS3_HUMAN, 399 amino acids (44.41 kDa).

bombolitin any of five structurally related peptides from the venom of the bumblebee, *Megabombus pennsylvanicus*, that are rich in hydrophobic amino-acid residues. They all lyse erythrocytes and liposomes, release histamine from mast cells, and stimulate phospholipase A_2; their properties are similar to those of **melittin**. Example, bombolitin I: database code BOL1_MEGPE, sequence IKTITTMLAKLGKVLAHV (1.836 kDa).

bombyxin any of a family of brain secretory peptides of the silkmoth that activate prothoracic glands to produce

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ecdysone. They contain an A and B chain joined by disulfide bonds, and are homologous to vertebrate insulins. Example, bombyxin A-9 (precursor): database code BXA9_BOMMO, 92 amino acids (10.29 kDa); residues 20–47 are the B chain, 73–92 the A chain.

bond **1** *or* **covalent bond** a region of high electron density between atoms that arises, at least partly, from sharing of electrons and gives rise to an attractive force and a characteristic internuclear distance between the atoms. *See* **coordination**, **dipolar bond**, **hydrogen bond**. **2** the representation of a covalent bond in an extended chemical formula. **3** to join or link together (esp. chemical entities); to **ligate** (def. 1).

bond angle the angle formed between two bonds at a given polyvalent atom.

bond-dissociation energy *see* **dissociation energy**.

bond energy **1** the average value of the gas-phase **bond dissociation energies** (usually at 298 K) of a given type of bond in the same chemical species: **mean bond energy**. **2** loosely, the free energy change occurring on hydrolysis of a hydrolysable chemical bond.

bonding the act or process of forming a covalent **bond** (def. 1); the state of being so linked. *See also* **domain of bonding**.

bond length the distance between the centres of the nuclei of two bonded atoms.

bone the hard, dense connective tissue that constitutes the skeleton of many animals. It consists of an organic matrix impregnated with bone mineral salts. The matrix is made up of 90–95% type I collagen, a small amount of proteoglycan, and a 49-residue protein containing three γ-carboxyglutamate residues, the formation of which is vitamin K-dependent. This protein binds strongly to the hydroxyapatite crystals of the bone mineral. The inorganic part of the bone consists largely of basic calcium phosphate, which is organized into small crystals of hydroxyapatite, 0.8–1.5 nm thick, 2–4 nm wide, and 20–40 nm long, of approximate composition $Ca_{10}(PO_4)_6(OH)_2$. Other anions present are carbonate, fluoride, hydroxide, and citrate. Most of the body's Mg^{2+}, about 25% of its Na^+, and a smaller proportion of its K^+ is found in bone.

bone GLA-protein (BGP) *see* **osteocalcin**.

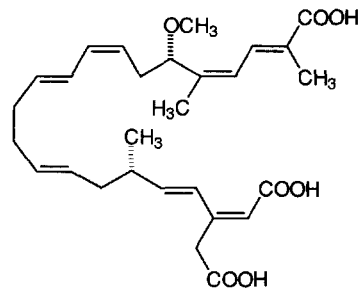
bone marrow the soft tissue contained within the internal cavities of bones. **Red marrow** (*or* myeloid tissue), found in developing bone, ribs, vertebrae, and in parts of the long bones, is actively hemopoietic and contains all the cells of the circulating blood and their precursors together with megakaryocytes, reticulum cells, macrophages, and plasma cells. In adult animals the marrow of many bones, particularly limb bones, becomes filled with fatty tissue known as **yellow marrow**. In adult mammals, B lymphocytes develop and differentiate in the bone marrow.

bone-marrow-derived cell any cell derived from bone marrow tissue, including erythrocytes, lymphocytes, granulocytes, etc. The term is often used misleadingly to refer to the **B lymphocytes**.

bone morphogenetic protein any of several zinc metalloendopeptidases enzyme belonging to the sub-subclass EC 3.4.24 and having an **EGF** motif repeat; they are members of the **astacin** subfamily.BMP enzymes are disulfide-linked homodimers of the transforming growth factor-β family and are related to **tolloid**. They are involved in induction of bone and cartilage formation. Example BMP-1 precursor from human: database code BMP1_HUMAN, 730 amino acids (82.81 kDa).

bone sialoprotein 1 *see* **osteopontin**.

bongkrekic acid 3-carboxymethyl-17-methoxy-6,18,21-trimethyldocosa-2,4,8,12,14,18,20-heptaenedioic acid; a toxic antibiotic formed by *Pseudomonas cocovenenans* grown on partially defatted coconut. It is named after 'bongkrek', a product of mouldy Indonesian coconut that becomes highly toxic when the *Pseudomonas* outgrows the mould. It is an inhibitor of oxidative phosphorylation, an effect ascribable to its inhibitory action on mitochondrial adenine nucleotide translocation, apparently by fixing the adenine nucleotides to the translocation sites thus rendering dissociation of the nucleotides from the translocator rate-limiting in the overall transport process. *Compare* **atractyloside**.



booster dose a second or subsequent dose of antigen, especially in the form of a vaccine, given after the priming dose with the object of stimulating rapid production of large amounts of antibody.

Born, Max (1882–1970), German-born British physicist; Nobel Laureate in Physics (1954) 'for his fundamental research in quantum mechanics, especially for his statistical interpretation of the wavefunction' [prize shared with W. W. G. F. Bothe].

Born equation an equation for the free energy change, ΔG, when a sphere of charge e and radius r is brought into a uniform medium of unvarying dielectric constant D:

$$-\Delta G = (1 - 1/D)(e^2/2r).$$

borohydride any member of a group of compounds with the structure MBH_4, where M is an alkali metal. These compounds will reduce aldehydes, ketones, and Schiff bases in nonaqueous solvents, and also acids, esters, acid chlorides, and nitriles. ^3H-labelled borohydrides are useful for the facile reductive tritiation of the aforementioned compounds.

boronyl the group $-B(OH)_2$; it is used attached to a matrix to complex with *cis*-diols (as in some saccharides).

borosilicate (glass) a silicate glass containing at least 5% boric oxide. Such a material has a high melting point and a low coefficient of thermal expansion, and hence is useful for the manufacture of heat-resistant glassware.

boss *symbol for* bride-of-sevenless gene (*see* **Sevenless protein**).

Bothe, Walther Wilhelm Georg Franz (1891–1957), German experimental physicist noted for his development (with H. Geiger) of the coincidence method of particle counting and for his discovery of the particle later identified as the neutron; Nobel Laureate in Physics (1954) 'for the coincidence method and his discoveries made therewith' [prize shared with M. Born].

bottom yeast *the popular name for* any of various strains of **brewers' yeast** that effect fermentation at a comparatively low temperature and tend to sediment to the bottom of the fermentation vessel. It is used for the manufacture of light beers, e.g. lager. Bottom yeast is generally distinguishable from **top yeast** by its ability to produce extracellular β-galactosidase, EC 3.2.1.23.

botulinus toxin a mixture of exotoxins formed by *Clostridium botulinum*, the causal agent of botulism, that is a potent inhibitor of acetylcholine release from cholinergic neurons, possibly by inactivation of actin involved in transmitter exocytosis. There are several types, depending on the strain of the producing organism; all comprise a disulfide-linked heterodimer of heavy (H) and light (L) chains. The L chain has the pharmacological activity and the B chain has domains that mediate channel formation (N terminus) and toxin binding (C terminus). Example, type A precursor: database code

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BXA_CLOBO, 1295 amino acids (149.15 kDa): amino acids 1–447 form the L chain and 448–1295 form the H chain.

Bouguer–Beer law *another name for* **Beer's law** (def. 1).

Bouguer's law a physical law stating the relation between the amount of light transmitted by an absorbing medium and its thickness, based upon the finding that successive equal thicknesses of sheets of glass absorbed equal fractions of the light incident upon them. It may be expressed in the form $I_{trs} = I_0 e^{-kd}$, where I_0 is the intensity of the incident light, I_{trs} is the intensity of the transmitted light, d is the thickness of the absorbing medium, and k is a constant. The law was later restated by Lambert — *see* **Lambert's law (of absorption)** — and extended to solutions by Beer — *see* **Beer's law** (def. 1). [After Pierre B. Bouguer (1698–1758), French astronomer and mathematician who discovered it in 1728.]

boundary any zone of transition, either between solvent and solution or between two solutions; i.e. a zone in which the composition of a solution changes.

boundary spreading the broadening of a boundary during ultracentrifugation of macromolecules due to the effects of diffusion.

bound-to-free ratio *abbr.*: B/F ratio; the ratio of the amount of a ligand bound by a specific macromolecule or receptor to the amount of ligand free in solution, in a specified system. Plotting [B]/[F] versus [F] yields a **Scatchard plot**.

bouvardin a cyclic hexapeptide isolated from the plant *Bouvarda ternifolia*, used as a drug against dysentery. It has antitumour properties and inhibits eukaryotic protein synthesis.

bovine of, belonging to, or characteristic of the ox tribe Bovini, which includes cattle, especially of the genus *Bos*.

bovine albumin *or* **bovine serum albumin** *see* **serum albumin**.

bovine pancreatic inhibitor *or* **bovine pancreatic trypsin inhibitor** *or* **basic protease inhibitor** a protein from cattle pancreas that inhibits trypsin, kallikrein, chymotrypsin, and plasmin. A popular molecule for studies on protein folding, etc., it contains three disulfide bonds. Database code: NRL_5PTI and others (e.g. NRL_1TGSZ with bound proteinase). The sequence is:

RPDFCLEPPYTGPCKARIIRYFYNAKAGLCQT-
FVYGGCRAKRNNFKSAEDCMRTCGGA.

(10.903 kDa). The 3-D structure is also known.

bovine spongiform encephalopathy *abbr.*: BSE; a transmissible dementia in cattle, sometimes also known as 'mad cow disease', characterized by a spongy degeneration of neuronal cells in the brain and also enlargement of the astrocytes therein. It appears to be caused by a **prion**, and original outbreaks were thought to be the result of feeding cattle on offal derived from sheep infected with **scrapie**.

Bowman–Birk inhibitor *see* **soybean trypsin inhibitor**.

Bowman's capsule *or* **glomerular capsule** the dilated, cup-shaped vesicle at the proximal end of a nephron that encloses a knot of blood capillaries constituting the glomerulus. It is the site of primary filtration of blood into the nephron. [After William Paget Bowman (1816–92), British histologist and ophthalmic surgeon.]

Boyden chamber an apparatus, consisting of two small chambers separated by a micropore filter, used in the study of chemotaxis.

Boyle's law *see* **gas laws**. [After Robert Boyle (1627–91), Irish chemist and physicist.]

bp *symbol for* base pair(s).

b.p. *abbr. for* boiling point.

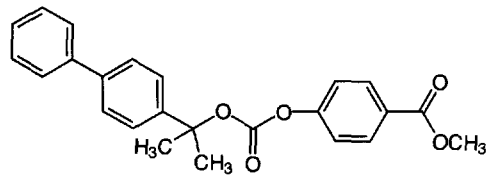
BP *abbr. for* **1** blood pressure. **2** British Pharmacopoeia.

BPC *abbr. for* British Pharmaceutical Codex.

B peptide *or* **fibrinopeptide B** the 20-residue peptide cleaved from the β chains of a fibrinogen molecule when it is converted into fibrin by the proteolytic action of thrombin.

BPG *abbr. for* 2,3-bis(phospho)-D-glycerate.

BPOC *abbr. for* biphenylisopropyloxycarbonyl-; an acid-labelling group for amino acids, introduced using, e.g., 2-(4-biphenylyl)-prop-2-yl 4′-methoxycarbonylphenylcarbonate (reagent structure shown).



Bq *symbol for* becquerel.

Br *symbol for* **1** bromine. **2** the butyryl group.

brachyurin EC 3.4.21.32; *other name*: collagenolytic proteinase; a serine proteinase that catalyses the hydrolysis of proteins with broad specificity for peptide bonds. It degrades native collagen at about 75% of the length of the molecule from the N terminus; it also shows low activity on small-molecule substrates of both trypsin and chymotrypsin. Example from *Uca pugilator* (fiddler crab): database code COGS_UCAPU, 226 amino acids (23.47 kDa).

bradykinin *or* **kinin-9** *abbr.*: BK; a vasoactive nonapeptide, H-Arg-Pro-Pro-Gly-Phe-Ser-Pro-Phe-Arg-OH, formed by the action of **plasma kallikrein**, which hydrolyses the sequence out of the plasma globulin **kininogen**. Glandular kallikrein cleaves kininogen one residue earlier to give the decapeptide Lys-bradykinin (kallidin, *abbr.*: Lys-BK). Met-Lys-bradykinin is also formed, perhaps by the action of leukocyte kallikrein. Pharmacologically important analogues include des-Arg^9 or BK_{1-8} and Ile-Ser-bradykinin (or T-kinin), [Hyp^3]bradykinin, and [Hyp^4]bradykinin. Bradykinin is formed in a variety of inflammatory conditions and in experimental anaphylactic shock. It is a powerful blood-vessel dilator, increasing vascular permeability and causing a fall in blood pressure; it is also a constrictor of smooth muscle. *See also* **lysine(arginine) carboxypeptidase**.

bradykinin receptor any membrane protein that binds bradykinin (BK) and mediates its intracellular effects. Two types of receptor are recognized: B_1 (previously BK_1), on which order of potency is des-Arg^9-bradykinin (*abbr.*: BK_{1-8}) = kallidin (Lys-BK) > BK; and B_2 (previously BK_2), with order of potency kallidin > BK >> BK_{1-8}. Hence, BK_{1-8} is a powerful discriminator. B_1 receptors are considerably less common than B_2 receptors, which are present in most tissues. The rat B_2 receptor is a seven-transmembrane-domain protein which has been shown on activation to stimulate phosphoinositide turnover. Examples: B_1, database code BRB1_HUMAN, 353 amino acids (40.44 kDa); B_2, database code BRB2_HUMAN, 364 amino acids (41.44 kDa).

Bragg **1 (Sir) William Henry Bragg** (1862–1942), father of W. L. Bragg (*see* def. 2), British experimental physicist remembered for his invention of the X-ray spectrometer named after him and particularly for his use of it in collaboration with his son in solving many problems of concerning the arrangement of atoms in crystals; Nobel Laureate in Physics (1915) jointly with W. L. Bragg 'for their services in the analysis of crystal structure by means of X-rays'. **2 (Sir) William Lawrence Bragg** (1890–1971), son of W. H. Bragg (*see* def. 1) British experimental physicist, born in Australia, remembered for his formulation of Bragg's law of X-ray diffraction and for the X-ray crystallographic studies in collaboration with his father that were thus made possible, for his subsequent concern with the application of X-ray crystallography to biological macromolecules, and for playing an important part in establishing molecular biology as an independent discipline; Nobel Laureate in Physics (1915) jointly with W. H. Bragg (*see* def. 1).

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Bragg's law a law stating that when a crystal is pictured as a set of reflecting planes uniformly spaced at a distance d and a beam of X-rays of wavelength λ strikes the crystal at an angle θ, reinforcement of the reflected waves occurs when $\sin \theta = n\lambda/2d$, where n is an integer known as the **order of reflection**. [After W. L. Bragg; *see* **Bragg** (*see* def. 2).]

brain-derived neurotrophic factor *abbr.*: BDNF; a protein that promotes the survival of neuronal populations located either in the central nervous system or directly connected to it. Example (precursor) from chicken: database code BDNF_CHICK, 246 amino acids (27.68 kDa).

brain natriuretic peptide *see* **natriuretic peptide**.

branch **1** a subdivision of the stem or the root of a plant; any smaller structure growing or arising from a larger one. **2** a side chain attached to the main chain of a molecular entity. **3** to form a branch; to bifurcate; to divide into offshoots. — **branched** *adj.*; **branching** *n.*

branched-chain describing any molecular entity with one or more **branches** (def. 2).

branched-chain α-keto-acid dehydrogenase *abbr.*: BCKDH; EC 1.2.4.4; *recommended name*: 3-methyl-2-oxobutanoate dehydrogenase (lipoamide); *other name*: 2-oxoisovalerate dehydrogenase. An enzyme that catalyses the conversion of α-oxo acids to acyl-CoA and CO_2. Thiamine diphosphate is a coenzyme. The enzyme consists of a multienzyme complex of branched chain α-keto-acid dehydrogenase (E1), lipoamide acyltransferase (E2), and lipoamide dehydrogenase (E3). Human enzyme details: E1 is a dimer of α and β subunits; precursor database code ODBA_HUMAN, 444 amino acids (50.16 kDa) and ODBB_HUMAN, 392 amino acids (43.07 kDa); E2 database code (precursor) ODB2_HUMAN, 482 amino acids (53.43 kDa).

branched-chain α-keto-acid dehydrogenase kinase *see* **[3-methyl-2-oxobutanoate dehydrogenase (lipoamide)] kinase**.

branched-chain oxo-acid dehydrogenase phosphatase *see* **[3-methyl-2-oxobutanoate dehydrogenase (lipoamide)]-phosphatase**.

branched polymer any polymer in which there are side chains attached to a main chain.

brancher-deficiency amylopectinosis *an alternative name for* type IV **glycogen disease**.

branching *(in nuclear physics)* the simultaneous existence of more than one disintegration pathway for a particular radionuclide.

branching enzyme EC 2.4.1.18; *recommended name*: 1,4-α-glucan branching enzyme; *systematic name*: 1,4-α-D-glucan: 1,4-α-D-glucan 6-α-D-(1,4-α-D-glucano)-transferase; *other names*: amylo-(1,4–1,6)-transglycosylase; corn starch branching enzyme II; amylo-transglycosylase; glucanotransferase; starch branching enzyme II; any 1,4-α-glucan branching enzyme that catalyses the transfer of a segment of 1,4-α-glucan chain to a primary C-6 hydroxyl group in a similar glucan chain. Branching enzymes fall into two types: the plant **Q-enzymes** and the mammalian enzymes, which are able to produce glycogen, a more highly branched molecule than the amylopectin produced in plants by Q-enzymes. The name should always be qualified, e.g. glycogen branching enzyme, amylopectin branching enzyme. Example from *Zea mays*: database code MZEGLUCTRN, 799 amino acids (90.42 kDa).

branch migration a proposed model to explain the occurrence of apparently branched DNA structures, as seen by electron microscopy, and their conversion into linear duplex DNA. The branched structures may form by association over parts of their lengths of three or more polynucleotide strands. The migration of the branch point is presumed to occur by displacement of a strand from its fellow in one branch by a strand in another. Such a process may occur in transcription or in recombination.

BRCA *BRCA1* and *BRCA2* either of two genes implicated in susceptibility to breast cancer. Up to 80% of women who inherit mutated forms of either gene develop breast cancer, and *BRCA1* mutations imply a high risk of ovarian cancer.

brdU *or* **BrdU** *abbr. for* bromodeoxyuridine (the symbol BrdUrd is recommended).

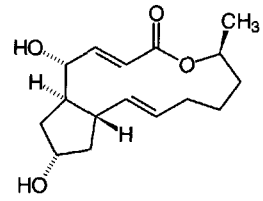
BrdUrd *symbol for* bromodeoxyuridine. *Compare* **BrUrd**.

breakage and reunion model the classical and generally accepted model of chromosomal crossing-over; it involves breakage of the chromatids and reunion of the alternative fragments.

breakpoint cluster region term originally suggested for a limited region of 5–6 kb in the base sequence of chromosome 22, in which breakpoints involved in formation of the **Philadelphia chromosome** were found to cluster. Molecular cloning of specific areas of DNA (e.g. band 22q11) gave a probe specific for the breakpoint translocation domain. Subsequent work led to this region being identified as the ***BCR*** gene.

breathing *a colloquial term for* transient dynamic changes in the structure of macromolecules involving expansion and contraction of the 3-D structure.

brefeldin A a fungal metabolite, isolated from *Penicillium brefeldianum*, that inhibits a wide variety of membrane transformations of importance in intracellular transport. It effects a rapid increase in the volume of Golgi cisternae and loss of recognizable Golgi apparatus in treated cells. There is a rapid reversible dissociation of a Golgi-associated peripheral protein identical with a coat protein subunit of non-clathrin-coated vesicles (β-COP). *See* **coatomer**.



B region the site of final epoxidation of carcinogenic polycyclic aromatic hydrocarbons. It is located on the terminal ring of the **bay region** on a bond adjacent to the bay region. *Compare* **A region**, **K region**, **L region**.

brei a finely and uniformly ground tissue suspension containing all the enzymes of the original material but with the normal spatial relationships between them disrupted. *Compare* **homogenate**.

bremsstrahlung the **X-rays** produced when an electrically charged particle, usually a β particle or an accelerated electron, is decelerated by the electric field of an atomic nucleus. The yield is directly dependent upon the magnitude of the atomic number of the target element. [German: braking radiation.]

brevetoxin any of the highly toxic lipid-soluble polyether compounds isolated from *Ptychodicus brevis* (*Gymnodinium breve*), the red-tide organism. They cause the death of fish and are responsible for shellfish poisoning in humans. They are activators of voltage-dependent Na^+ channels.

brevin *an alternative term for* **gelsolin**.

brevinin a secreted amphibian peptide with antibacterial and hemolytic activities. Example, brevinin-1 from *Rana brevipoda porsa*: database code BR1_RANBP, sequence

FLPVLAGIAAKVVPALFCKITKKC.

brewers' yeast *the common name for* strains of the yeast *Saccharomyces cerevisiae* that are used in brewing. In addition to their ability to produce, and remain viable under, appreciable levels of ethanol, such strains are able to ferment maltose, maltotriose, and other sugars in the wort, and to withstand its relatively high osmotic pressure. *See also* **bottom yeast**.

bridge *(in chemistry)* a valence bond, atom, or unbranched chain of atoms connecting two different parts of a molecule.

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bridgehead *(in chemistry)* either of the two atoms, e.g. tertiary carbon atomks, that are connected by a **bridge**.

bridge-receptor any molecular entity with two or more specific binding sites able to interact with and join a corresponding number of complementary ligands, which may or may not be the same.

Briggs–Haldane theory an alternative to the Michaelis–Menten theory of the kinetics of enzyme reactions for cases where breakdown of the enzyme–substrate complex to products is not slow in comparison with its dissociation to enzyme and substrate. *Compare* **Michaelis kinetics**. [After George Edward Briggs (1893–1985), British plant physiologist, and John Burdon Sanderson Haldane (1892–1964), British enzymologist, geneticist, philosopher, and popularizer of science, who put forward their theory in 1925.]

Brij *proprietary name for* any of a series of polyethylene ethers of higher fatty alcohols. They are surfactants useful for the solubilization of membrane fractions. Brij 35 is polyoxyethylene (23) lauryl ether, aggregation number 40, CMC 92 μM.

British antilewisite *abbr.*: BAL; *another name for* **dimercaprol**.

British thermal unit *abbr.*: Btu; a non-SI unit given by the energy required to raise the temperature of 1 pound of water through 1 °F. Since this depends on the temperature of the water, the temperature range should be specified. The Btu(mean), defined as the 1/180 part of the energy required to raise the temperature of 1 pound of water from 32 °F to 212 °F, is equal to 1055.06 J.

Brk *abbr. for* Bek-related kinase; *an alternative name for Cek2. See* ***Cek***.

BRN a family of neurally expressed genes encoding brain-specific transcription factors. They contain a **POU domain**. Brn-3.1 and Brn-3.2 modulate the terminal differentiation of auditory and visual system development respectively. Example, Brn-1 from *Mus musculus*: database code BRN1_MOUSE, 495 amino acids (50.01 kDa).

broad host range relating to the ability of a plasmid to be subjugated as a vector in a broad range of hosts, especially Gram-negative bacteria. Such plasmids are also termed promiscuous.

broad-spectrum antibiotic any antibiotic that is active against a wide range of bacterial species.

Brockmann body a discrete organ, occurring in fish, that contains tissue corresponding to that found in the islets of Langerhans of mammals. One or more Brockmann bodies occur in various teleost species. They are free of pancreatic acinar tissue, which makes them particularly suitable for biochemical studies and a good source of fish insulin. The principal islet weighs in the region of 1–50 mg; smaller secondary islets may also occur.

Brodie's fluid a **manometer fluid** containing 23 g NaCl, 5 g sodium tauroglycerate, 100 mg Evan's Blue, and a few drops of an ethanolic thymol solution, in 1000 mL of water; D = 1.033. The standard pressure (760 mmHg) in mm of manometer fluid is 10 000.

brom+ *a variant form of* **bromo+**.

bromelain *or* **bromelin** either of two similar **cysteine proteinases**: **stem bromelain**, EC 3.4.22.32, isolated from the stem of the pineapple, *Ananas comosus*; and **fruit bromelain**, EC 3.4.22.33, from the same plant. They are broad-specificity proteinases, similar to other cysteine proteinases but with so far unique geometry and reactivity at the active site. The two types of enzyme are distinguished by the substrate Z-Arg-Arg-NHMec, which is hydrolysed by stem bromelain but not by fruit bromelain. Stem enzyme: database code BROM_ANACO, 212 amino acids (22.81 kDa).

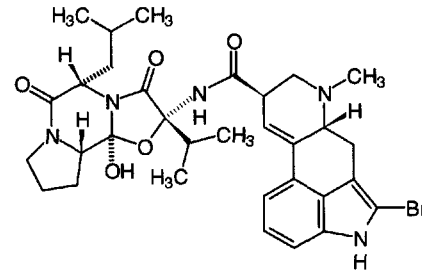
bromination the introduction of one or more bromine atoms (bromo residues) into an organic molecule, whether by addition or substitution. —**brominate** *vb*.

bromine *symbol*: Br; a halogen element of group 17 of the IUPAC **periodic table**; atomic number 35; relative atomic mass 79.909. Natural bromine consists of the two isotopes ^{79}Br and ^{81}Br at almost equal relative abundances.

bromine-82 the radioactive nuclide $^{82}_{35}$Br; half-life 35.3 h; it emits beta radiation (0.444 MeV) and gamma radiation of various energies.

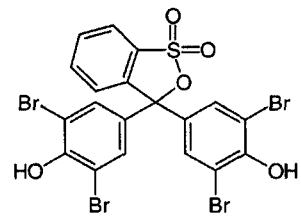
bromo+ *or (sometimes before a vowel)* **brom+** *prefix* denoting a bromine atom in organic linkage.

bromocriptine *or* **bromoergocriptine** 2-bromoergocryptine; an ergotoxin **ergot** alkaloid derivative that acts as a dopamine (D_2) receptor agonist. It inhibits the secretion of prolactin and somatotropin by the pituitary gland, and has potential applications in the treatment of Parkinson's disease.

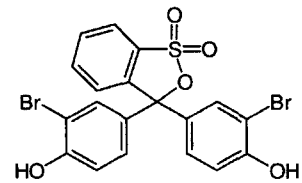


bromodeoxyuridine *symbol*: BrdUrd; 5-bromo-2′-deoxyuridine; 5-bromouracil 2′-deoxyriboside; a synthetic analogue of thymidine. It acts as an inhibitor of cell differentiation, and also has antiviral properties. *See* **bromouracil**.

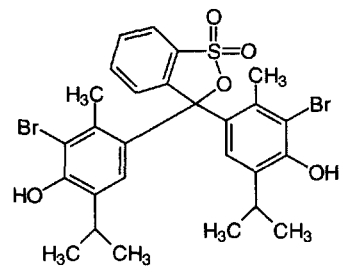
Bromophenol Blue a dye used as a pH indicator, changing from yellow to blue over the pH range 3.0–4.6



Bromophenol Red a dye used as a pH indicator, changing from yellow to red over the pH range 5.2–6.8



Bromothymol Blue a dye used as a pH indicator, changing from yellow to blue over the pH range 6.0–7.6



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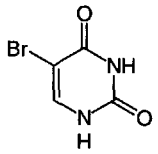
bromouracil *symbol*: BrUra; 5-bromouracil; 5-bromo-2,4(1*H*,3*H*)-pyrimidine-dione; a synthetic analogue of thymine with mutagenic activity. It is incorporated into DNA as **bromodeoxyuridine**, which replaces thymidine and induces transitions of G–C base-pairing to A–T pairing. It can be used as a density marker for DNA. The free compound is an inhibitor of dihydrouracil dehydrogenase.



bromouridine *symbol*: B *or* BrUrd; 5-bromouridine; 5-bromouracil riboside; a synthetic analogue of ribothymidine.

Brønsted catalysis law an expression of the relation between the rate constant, k, of a catalysed reaction, and the pK of the catalyst: $\log k = c + b\mathrm{p}K$, where b and c are constants and the value of b provides a measure of the balance between nucleophilic and general base character of the catalysis. [After Johannes Nicolaus Brønsted (1879–1947), Danish physical chemist.]

Brønsted–Lowry acid any chemical species capable of donating a hydron to a base. Examples are H_2O, H_3O^+, CH_3COOH, $H_2PO_4^-$, NH_4^+. [After J. N. Brønsted (*see* **Brønsted catalysis law**) and Thomas Martin Lowry (1874–1936), British chemist.]

Brønsted–Lowry base any chemical species capable of accepting a hydron from an acid. Examples are OH^-, H_2O, CH_3COO^-, HPO_4^{2-}, NH_3.

Brookhaven database *see* **PDB**.

broth *(in bacteriology)* any liquid culture medium, especially nutrient broth.

Brown, Michael Stuart (1941–), US physician and molecular geneticist notable for his discovery (in collaboration with J. L. Goldstein) of cellular receptors for low-density lipoproteins and their role in the removal of cholesterol from the bloodstream; Nobel Laureate in Physiology or Medicine (1985) jointly with J. L. Goldstein 'for their discoveries concerning the regulation of cholesterol metabolism'.

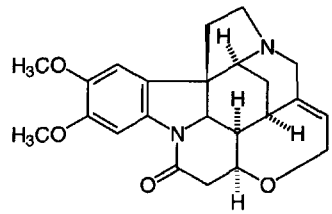
brown adipose tissue a highly specialized tissue with a high content of lipid and cytochromes found in some animals, particularly hibernating animals and the newborn of some species. It is highly vascular and consists of small polygonal cells, each containing many separate lipid droplets and many mitochondria. Its function is thermogenesis during the arousal period after hibernation or, in the young, to provide heat before shivering has developed. It is active also in normal but not in obese humans. The colour is due to the high cytochrome content. Heat is generated by lipid oxidation through electron transport not coupled to oxidative phosphorylation. The uncoupling is mediated by **brown fat uncoupling protein**. *Compare* **white adipose tissue**.

brown fat uncoupling protein *abbr.*: UCP; *other names*: mitochondrial UCP; thermogenin; a dimeric integral mitochondrial inner membrane protein that forms an H^+-channel, is unique to brown adipose tissue mitochondria, and is important for thermogenesis of this tissue. By causing the membrane to leak protons, it abolishes the proton gradient that drives oxidative phosphorylation, so that electron transport results solely in heat production. Example from mouse: database code UCP_MOUSE, 306 amino acids (33.08 kDa).

Brownian movement the peculiar random movements shown by microscopic particles in a disperse phase, i.e. when suspended in a liquid or gas. It is caused by the continuous irregular bombardment by the molecules of the surrounding medium. [After Robert Brown (1773–1858), British botanist who first observed it in 1827.]

browning reaction any of a group of complex reactions, both enzymic and nonenzymic, that occur in some foods during processsing and/or storage and cause a brownish discoloration. Members of this group include the oxidation of phenolic compounds (which is believed to be enzymic) together with caramelization, ascorbate decomposition, and the **Maillard reaction** (all of which are believed to be nonenzymic).

brucine 2,3-dimethoxystrychnidin-10-one; a highly toxic bitter-tasting alkaloid obtained from *Strychnos* seeds. It is used as a resolving agent for some racemates. *Compare* **strychnine**.

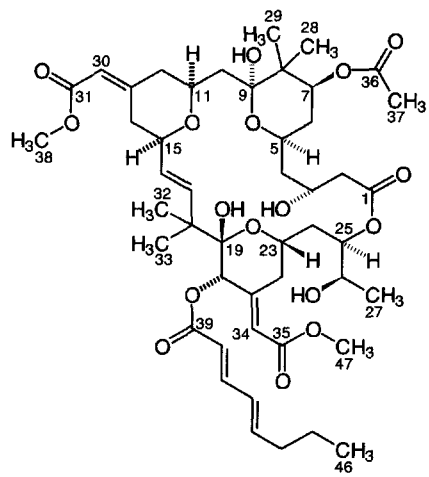


BrUra *symbol for* bromouracil.

BrUrd *symbol for* bromouridine (alternative to B). *Compare* **BrdUrd**.

brush border the dense covering of **microvilli** on the apical surface of epithelial cells in the intestine and kidney. The microvilli aid absorption by increasing the surface area of the cell.

bryostatin any of a number of highly potent activators of protein kinase C found in bryozoans, especially *Bugula neritina*. They were isolated as the active anti-leukemic agent of bryozoan extracts. They block phorbol ester-induced differentiation of human promyelocytic leukemia cells and other actions of phorbol esters.



bryostatin 1

BSA *abbr. for* bovine serum albumin. *See* **serum albumin**.

BSE *abbr. for* bovine spongiform encephalopathy.

B side the side of the nicotinamide ring of NADH or NADPH at which projects the *pro-S* hydrogen atom (known as H_B) at the 4 position. *Compare* **A side**.

BTEE *abbr. for N*-benzoyl-L-tyrosine ethyl ester (a substrate for the assay of chymotrypsin).

B-transferase EC 2.4.1.37; *recommended name*: fucosylglyco-

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protein 3-α-galactosyltransferase; *other name*: [histo-blood group] B transferase; an enzyme that catalyses the reaction:

UDPgalactose + glycoprotein α-L-fucosyl-(1,2)-D-galactose = UDP + glycoprotein α-D-galactosyl-(1,3)-[α-L-fucosyl-(1,2)]-L-galactose,

thus adding galactose to the H antigen of the **ABH antigen** system, leading to formation of the B antigen. The protein is a product of one allele of the *ABO* gene. It has virtual identity of sequence with that catalysing **A-transferase** activity, differing only at residues 176 (A has Arg, B has Gly), 235 (A Gly, B Ser), 266 (A Leu, B Met), and 268 (A Gly, B Ala). Database code BGAT_HUMAN, 354 amino acids (40.89 kDa).

Btu *abbr. for* British thermal unit.

Bu *symbol for* the butyl group.

BU *(sometimes) abbr. for* bromouracil (BrUra is recommended).

bubble column a column-shaped bioreactor in which the reaction medium is kept mixed and aerated by the introduction of air at the bottom.

Büchner, Eduard (1860–1917), German chemist and biochemist renowned for his seminal discovery that alcoholic fermentation could be initiated with a cell-free press juice from brewers' yeast, the active principle of which he considered to be a protein denoted zymase; Nobel Laureate in Chemistry (1907) 'for his biochemical researches and his discovery of cell-free fermentation'.

Büchner funnel a cylindrical funnel for filtration, usually of porcelain or plastic, that includes a perforated plate on which a filter paper is placed. It is generally used with a vacuum. *See also* **Hartley filter funnel**.

bud **1** a small lateral or terminal protuberance on the stem of a plant that contains undeveloped foliage or floral leaves. **2** a budlike protuberance on the surface of a yeast cell or other simple organism. **3** to form a bud. **4** to reproduce asexually, as in yeasts, by the process of **budding**.

Buddha suite of computer programs for structure refinement and energy minimization.

budding **1** the production of a bud or buds. **2** a form of asexual reproduction, occurring in certain bacteria and fungi (e.g. yeasts) and some primitive animals in which an individual arises from a daughter cell formed by pinching off a part of the parent cell. The budlike outgrowths so formed may sometimes remain attached to the parent cell.

BUdR *or* **BUDR** *(sometimes) abbr. for* bromodeoxyuridine (the symbol BrdUrd is preferred).

bufadienolide any of various naturally occurring doubly unsaturated lactones of certain steroids with important pharmacological effects on heart muscle (*see* **cardiac glycoside**). They are so named because they were originally found in the venomous secretion of the skin glands of some toads (*Bufo*), and are hence also known as **toad poisons**. They also occur in certain plants, e.g. *Digitalis*. *See also* **bufogenin B**.

buffer **1** any substance or mixture of substances that, when dissolved (usually in water), will maintain its solution at approximately constant pH despite small additions of acid or base. The commonest examples are moderately strong solutions containing both a weak acid and its conjugate base (or a weak base and its conjugate acid). A substance is useful as a buffer over a range of about one pH unit either side of its pK, but is most effective at or near the pK. Buffer substances used for biochemical or biological purposes include: acetate, bicarbonate, bis-tris propane, borate, citrate, dimethylmalonate, glycinamide, glycylglycine, imidazole, phosphate, succinate, and **Tris** together with any **Good buffer substances**. By extension, the term may be applied to agents controlling the activities of various other specified entities, e.g. redox buffer, carbon-dioxide buffer, metal-ion buffer. Also used attributively: e.g. buffer action; buffer salt; buffer solution. **2** a solution of a **buffer** (def. 1). **3** a short-term storage facility (e.g. as part of the memory of a computer), especially one whose patterns or rates of input and output can differ. **4** to treat with or to incorporate a buffer (def. 1); to act as a buffer. *See also* **buffering capacity, buffer value**. —**buffered** *adj.*; **buffering** *n.*

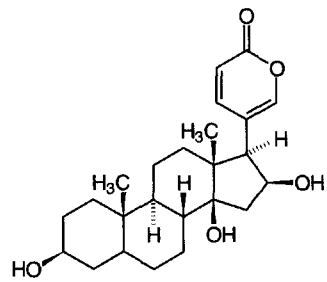
buffering capacity *or* **buffering power** **1** the number of gram-equivalents of either hydrogen ions or hydroxide ions required to change the pH of 1 litre of 1 M buffer solution by one unit. Buffering capacity = $(1/m)$ (dn/dpH), where m is the number of moles of buffer, and dpH is the pH change produced by addition of dn equivalents of hydrogen ions or hydroxide ions. **2** *an alternative term for* **buffer value**.

buffer solution *see* **buffer** (def. 2).

buffer value *or* **Van Slyke buffer value** *or* **buffering capacity** *symbol*: β; the amount of acid or base, in gram-equivalents, needed to change the pH of 1 litre of a buffer solution by one unit at any pH; i.e. β = db/dpH, where b is the molar concentration of base in the solution. [After Donald Dexter Van Slyke (1883–1971), US biochemist, who described it in 1922.]

buffy coat the layer of white cells that forms between the layer of red cells and the plasma when unclotted blood is centrifuged or allowed to stand.

bufogenin B 3β,14,16β-trihydroxy-5β-bufa-20,22-dienolide; a **bufadienolide** found in the Chinese drug Ch'an Su, prepared from Chinese toads (*Bufo asiaticus*).



bulge loop a structure in a polynucleotide duplex in which one strand contains a nonterminal extra sequence that is not able to base-pair with the second strand, thereby forming a bulge on one side of the duplex.

BUN *abbr. for* blood urea nitrogen, an index of the blood-urea concentration.

bundle sheath a parenchymal sheath surrounding a vascular bundle in plants.

bungarotoxin any of various neurotoxins derived from the venom of the elapid snake, *Bungarus multicinctus*. The chief components are: (1) α bungarotoxin, a single polypeptide chain of 74 amino-acid residues; it is an irreversible antagonist of nicotinic cholinergic receptors and causes paralysis; (2) β bungarotoxin, a multicomponent protein composed of two polypeptide chains: a long chain (120 amino-acid residues) and a short chain (60 residues); it prevents the release of acetylcholine from cholinergic neurons.

Bunsen coefficient *symbol*: α; the absorption coefficient of a gas in a solution. It is defined as the volume of gas in litres, reduced to 273.15 K and 1 atm (101 325 Pa) pressure, that dissolves in 1 litre of liquid when the partial pressure of the gas in the gas phase is 1 atm. [After Robert Wilhelm Bunsen (1811–99), German chemist.]

bunyavirus any of a group of RNA animal viruses consisting of enveloped particles, 90–100 nm in diameter with helical nucleocapsids, and containing segmented RNA (minus strand) of 3–4 MDa. The group has been recognized as different from **togaviruses** and includes arthropod-borne viruses that can cause encephalitis.

buoyant density the density of a solute molecule as determined by density-gradient ultracentrifugation. It is the density of the solution, ρ, at the point in the gradient where: $\rho = 1/\gamma$, where γ is the **partial specific volume** of the solute in question.

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buoyant force *symbol*: F_B; the force acting on an object suspended in a liquid due to the liquid displaced by the object. It is given by: $F_B = V_P \rho_M g$, where V_P is the volume of the object, ρ_M is the density of the displaced liquid M, and g is the acceleration due to gravity.

burette *or (US)* **buret** a graduated (often glass) tube with a pinch-clamp, stopcock, or valve at one end used for measuring or dispensing known volumes of fluids, especially liquids. A graduated syringe used for the same purpose may also be termed a burette.

Burkitt's lymphoma a malignant tumour of the lymphatic system, most commonly affecting children in tropical Africa within 15° north and south of the Equator. **Epstein–Barr virus** can be demonstrated in a proportion of cultured tumour cells though it is unlikely that the virus is the sole cause of the malignancy. [After Denis Parsons Burkitt (1911–93), British surgeon.]

Burnet, (Sir) Frank Macfarlane (1899–1985), Australian physician, virologist, and immunologist notable in particular for formulation of the clonal selection theory of acquired immunity; Nobel Laureate in Physiology or Medicine (1960) jointly with P. B. Medawar 'for discovery of acquired immunological tolerance'.

Burnet's theory of immunity *see* **clonal selection theory**.

bursacyte *an alternative name (archaic) for* **B lymphocyte**.

bursa of Fabricius *or* **cloacal bursa** a saclike lymphoepithelial structure opening into the dorsal part of the cloaca in young birds. It usually degenerates as the birds reach maturity. It is associated with humoral immunity and the lymphocytes processed by it are termed **B lymphocytes**. In mammals it is likely that hemopoietic tissue itself fulfils the equivalent role, providing the appropriate microenvironment for the maturation of B lymphocytes from precursor stem cells.

bursectomy removal of the **bursa of Fabricius**, either by surgery *in ovo* or shortly after hatching, or by destruction *in ovo* by application of, e.g., testosterone. Bursectomy inhibits the formation of **B lymphocytes** and hence circulating antibody.

bursin the tripeptide Lys-His-Gly-NH_2; a selective B-cell differentiating hormone from the bursa of Fabricius of chickens.

burst **1** the initial pre-steady-state liberation of the first product, B, in an enzymic reaction of the type: $E + AB = EAB \rightarrow EA + B$ and $EA \rightarrow E + A$, where E is the enzyme and A is the second product. **2** the sudden release of phage particles accompanying lysis of a phage-infected bacterial cell. *See also* **burst size, respiratory burst**.

burst size the mean number of bacteriophage particles set free per infected bacterium upon lysis of phage-infected cells.

butanediol fermentation a type of fermentation effected by some members of the Enterobacteriaceae, e.g. *Enterobacter*, *Erwinia*, *Klebsiella*, and *Serratia*, in which glucose is fermented with the production of 2,3-butanediol and other substances.

butanoyl *another name for* **butyryl**.

Butenandt, Adolf Friedrich Johann (1903–95), German organic chemist and biochemist renowned for his pioneering studies of steroid hormones and pheromones, especially for his isolation and determination of the structures of the first sex hormones (androsterone, estrone, and progesterone) and the first insect hormone (ecdysone), and for the isolation of the first pheromone (bombykol); Nobel Laureate in Chemistry (1939) 'for his work on sex hormones' [prize shared with L. Ružička].

butyl *symbol*: Bu; the alkyl group, CH_3–$[CH_2]_2$–CH_2–, derived from butane.

butyl-PBD *see* **biphenylylphenyloxadiazole**.

butyrate **1** *trivial and preferred name for* **butanoate**; the anion CH_3–$[CH_2]_2$–COO^-, derived from butyric acid (butanoic acid), a saturated, unbranched, aliphatic acid. **2** any mixture of free butyric acid and its anion. **3** any salt or ester of butyric acid.

butyric acid fermentation a type of fermentation effected by some saccharolytic species of *Clostridium*, e.g. *C. butyricum*, in which glucose is fermented, with the production of acetic acid, butyric acid, carbon dioxide, and dihydrogen.

butyrophenone any of a group of antipsychotic drugs, e.g. **haloperidol**, that are more selective than the **phenothiazine** group. Butyrophenones interact rather more specifically with dopamine D_2 receptors and reduce the firing of dopaminergic neurons.

butyrophilin a type I **membrane protein** of mammary gland, probably involved in stimulating the secretion of droplets of fat in milk. Example (bovine, precursor): database code BUTY_BOVIN, 526 amino acids (59.20 kDa).

butyryl *symbol*: Br; *trivial and preferred name for* **butanoyl**; the acyl group, CH_3–$[CH_2]_2$–CO–, derived from butyric acid (butanoic acid).

BX-C *abbr. for* the bithorax complex, one of two (*see* **ANT-C**) major families of **homeotic genes** in *Drosophila*, mutations in which affect thoracic and abdominal segments.

byte a single unit of information handled by a computer; the binary unit required for storage of a character, usually comprising eight **bits**.

Bz *symbol for* the benzoyl group.

bZIP *abbr. for* basic zipper; a fingerprint of a family of proteins, named after their two main features: a basic region (b) and a **leucine zipper** domain (ZIP). The basic region harbours a DNA-contact surface, and the leucine zipper domain is essential for homodimer formation or formation of heterodimers with other leucine zipper proteins. The family includes the **AP**, **ATF**, and **CREB protein** transcription factors.

Bzl *symbol for* the benzyl group.

BZLF1 one of a group of transcription factors related to the *jun* and *fos* gene products. It is involved in the switch from latency to virus-particle production following infection by **Epstein–Barr virus**. Database code BZLF_EBV, 245 amino acids (26.83 kDa).

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Cc

c **1** *symbol for* **a** centi+ (SI prefix denoting 10^{-2}). **b** **cyclic** (def. 3) or **cyclo+** (denoting cyclic compounds, as in cAMP for cyclic AMP or Hx_c for cyclohexyl. **c** *(obsolete)* **curie** (use Ci). **2** *abbr. for* **a** complementary (as in **cDNA**). **b** ***cis*** (not recommended). **c** *(obsolete)* cubic (i.e. to the third power).

c- *(in genetics) prefix* denoting cellular, as in c-*myc*, the cellular as opposed to viral (v-) version of a (proto)oncogene; *see*, e.g., ***MYC***.

c *symbol for* **1** amount-of-substance concentration; that for a particular substance may be denoted by adding a subscript, e.g. c_B for amount concentration of a substance B. **2** speed (alternative to *v*, *u*, or *w*). **3** (bold italic) velocity (alternative to ***v***, ***u***, or ***w***).

c- *abbr. for* ***cis-***.

c_0 *symbol for* speed of light *in vacuo*. The subscript may be omitted when there is no risk of ambiguity.

C **1** *symbol for* **a** carbon; *see* **carbon-11**, **carbon-12**, **carbon-13**, **carbon-14**. **b** designating a specific carbon atom, e.g. C-1, C-2. **c** a residue of the α-amino acid L-cysteine (or L-half-cysteine) (alternative to Cys). **d** a residue of the base cytosine in a nucleic acid sequence. **e** a residue of the ribonucleoside cytidine (alternative to Cyd). **f** **coulomb**. **g** *or (formerly)* C′ complement (the main components of complement are designated C1–C9). **2** a high-level computer language based on function evaluation and much used in the development of computer software for molecular biology.

°C *symbol for* degree Celsius (*formerly* degree centigrade). *See* **Celsius temperature**.

C_H *symbol for* the constant region of an immunoglobulin **heavy chain**. The particular constant domain in question may be indicated as C_H1, C_H2, C_H3.

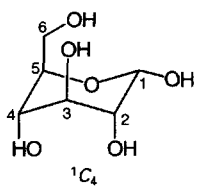
C_L *symbol for* the constant region of an immunoglobulin **light chain**.

C *symbol for* **1** capacitance. **2** heat capacity (C_p at constant pressure, C_V at constant volume, C_m molar heat capacity). **3** number concentration (C_B for a substance B).

C- *(in chemical nomenclature)* a locant indicating substitution on carbon; a particular carbon atom may be specified by a right superscript.

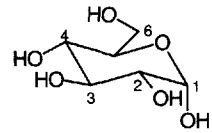
-C a conformational descriptor designating the **chair conformation** of a six-membered ring form of a monosaccharide or monosaccharide derivative. Locants of ring atoms that lie on the side of the structure's reference plane from which the numbering appears clockwise are indicated by left superscripts and those that lie on the other side of the reference plane by right subscripts; e.g. $-{}^1C_4$, $-{}^4C_1$. *See also* **conformation** (def. 2).

$-{}^1C_4$ *or (formerly)* **-1*C*** conformational descriptor for an aldopyranose in the chair conformation, with C2, C3, C5, and O5 in the structure's reference plane, and with C1 above and C4 below the plane; e.g. α-D-glucopyranose-$^1C_4$.



$^1C_4$

$-{}^4C_1$ *or (formerly)* **-*C*1** a conformational descriptor for an aldopyranose in the chair conformation, with C2, C3, C5, and O5 in the structure's reference plane, and with C1 below and C4 above the plane; e.g. α-D-glucopyranose-$^4C_1$.



$^4C_1$

Ca *symbol for* calcium.

CAA a codon in mRNA for L-glutamine.

CAAT box *or* **CAT box** a conserved sequence in DNA found within the **promoter** region of the protein-encoding genes of many eukaryotes. It has the consensus sequence GGCCAATCT and is believed to determine the efficiency of transcription from the **promoter**.

Cab-O-Sil *proprietary name for* **fumed silica** supplied by Cabot Carbon Ltd.

CaBP3 *see* **calreticulin**.

CAC a codon in mRNA for L-histidine.

cachectic factor a 24 kDa proteoglycan isolated from the murine adenocarcinoma MAC16 that has been implicated in the production of **cachexia**. The peptide has the N-terminal sequence YDPEAASAPGSGDPSHEA and has *N*- and *O*-glycans. Intravenous injection of the proteoglycan produces rapid weight loss.

cachectin *see* **cachexia**, **tumour necrosis factor-α**.

cachexia a condition caused by chronic disease, such as cancer, and characterized by wasting, emaciation, feebleness, and inanition. It led to the name 'cachectin' for the protein now known as **tumour necrosis factor** but a 24 kDa proteoglycan has more probably been implicated in this. *See* **cachectic factor**.

cacodylate **1** dimethyl arsinate, the anion $(CH_3)_2$–$AsOO^-$ derived from cacodylic acid. It is useful as a buffer substance (pK_a = 6.2). **2** any salt of cacodylic acid.

cadaverine 1,5-pentanediamine; a substance formed by microorganisms in decaying meat and fish by the decarboxylation of lysine. It also occurs as an intermediate in the biosynthesis, via lysine, of some quinolizidine alkaloids (e.g. lupinine) in plants.

cadherin any member of a family of calcium-dependent cell adhesion proteins that preferentially interact in a homophilic manner in cell–cell interactions. Cadherins may thus contribute to the sorting of heterogeneous cell types; they are type I **membrane proteins**. The names of different classes indicate the tissues in which they were first found: E-cadherin is present on many types of epithelial cells; N-cadherin is present on nerve, muscle, and lens cells; and P-cadherin is present on placental and epidermal cells. Typically, cadherins have five similar extracellular domains, the outermost three of which have Ca^{2+}-binding sites, and an intracellular C-terminal domain that interacts with the actin cytoskeleton. Examples (all human) E-cadherin precursor: database code CADE_HUMAN, 882 amino acids (97.35 kDa); N-cadherin precursor: database code CADN_HUMAN, 906 amino acids (99.75 kDa); P-cadherin precursor: database code CADP_HUMAN, 829 amino acids (91.32 kDa); three motifs.

cadmium mycophosphatin a cadmium-binding phosphoglycoprotein, M_r 12 000; it lacks sulfur-containing amino acids, but is rich in aspartic and glutamic acids and phosphoserine.

CAD protein a multifunctional protein found in many eukaryotes and containing domains for three enzymes of pyrimidine biosynthesis: **carbamoyl phosphate synthase** (glutamine-hydrolysing); **aspartate transcarbamylase**; and **dihydroorotase**. Ex-

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ample from *Drosophila melanogaster*: database code PYR1_DROME, 2236 amino acids (248.95 kDa).

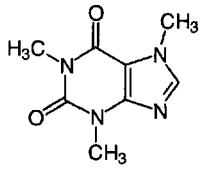
Caenorhabditis elegans a nematode (roundworm), with a genome of about 97 million base pairs. Its cellular anatomy has been fully described, and the nucleotide sequence of the genome determined, revealing over 19 000 genes, 40% of the predicted protein products having significant matches in other organisms.

caerulein *the Brit. spelling of* **cerulein**.

caeruloplasmin *the Brit. spelling of* **ceruloplasmin**.

caesium *alternative spelling (esp. Brit.) for* cesium.

caffeine 1,3,7-trimethylxanthine, 3,7-dihydro-1,3,7-trimethyl-1*H*-purine-2,6-dione; a substance found in certain plants, notably in tea and coffee and the beverages derived from them. It is an adenosine (A_1 and A_2) receptor antagonist and phosphodiesterase inhibitor, and a stimulant of the central nervous system, affecting the cardiovascular system and causing diuresis. Its actions are similar to those of **theophylline** but less potent.



caffetannic acid *an alternative name for* **chlorogenic acid**.

CAG a codon in mRNA for L-glutamine.

cage carrier *see* **ionophore**.

cage compound **1** *an alternative name for* **clathrate** (def. 1). **2** any compound possessing a nonplanar bicyclic or polycyclic molecular structure that encloses a cavity.

caged ATP a type of protected ATP analogue, e.g. adenosine-5′-triphospho-1-(2-nitrophenyl)ethanol (or the methanol-containing equivalent), that releases ATP in good yield when photolysed by a short pulse of light of 360 nm wavelength. Similarly, guanosine-5′-triphospho-1-(2-nitrophenyl)ethanol is used as **caged GTP**. These compounds can be introduced into cells prior to photolysis. Caged ATP has been used, e.g., to study muscle contraction on the millisecond timescale.

caged GTP *see* **caged ATP**.

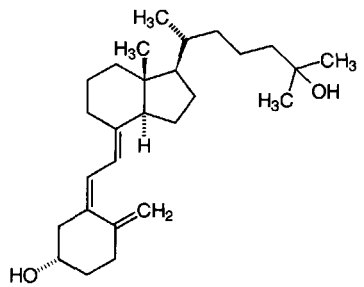
Cahn–Ingold–Prelog rule *or* **Cahn–Ingold–Prelog system** *an alternative name for* **sequence rule**.

cal *symbol for* calorie.

calbindin *other names*: cholecalcin; calbindin D9K; CABP; vitamin D-dependent calcium-binding protein; an **EF-hand** Ca^{2+}-binding protein from intestine. It is present in a variety of cells, including absorptive cells of the duodenum (in which its synthesis is vitamin D_3-dependent), in hippocampal cells, and in kidney. Example from *Rattus norvegicus*: database code CABI_RAT, 78 amino acids (8.90 kDa). Example from human: database code CABI_HUMAN, 78 amino acids (8.88 kDa).

calcemic factor *or (esp. Brit.)* **calcaemic factor** the prohormone of **parathyrin**.

calcidiol *the recommended trivial name for* calcifediol, 25-hydroxycholecalciferol. It is formed in liver from cholecalciferol, and is the major store of the vitamin in the body, being present largely in plasma. It is the precursor of the hormonal form of the vitamin, calcitriol. *See also* **vitamin D**.



calciductin *a name proposed for a* 23 kDa sarcolemmal protein that, when phosphorylated by a cAMP-dependent protein kinase, causes an approximately two-fold stimulation of the slow Ca^{2+} inward current.

calcifediol 25-hydroxyvitamin D_3; *another name for* **calcidiol**. *See also* **vitamin D**.

calciferol *an alternative (older) name for* **ergocalciferol**, also known as vitamin D_2. *See also* **vitamin D**.

calcification the deposition of calcium salts in the tissues. It is part of the normal process of bone formation in which **hydroxyapatite** crystals are deposited, in the neighbourhood of osteoblast cells, in a pre-existing collagen-containing matrix.

calcified describing a tissue that has been solidified by deposition of calcium; having undergone **calcification**.

calcimedin *see* **annexin**.

calcimycin *see* **A23187**.

calcineurin *or* **protein phosphatase 2B** (*abbr.*: PP-2B) *or* **CaM-BP$_{80}$** a major heat-labile calmodulin-binding protein isolated from bovine brain but later found in all cells from yeast to mammals. It has protein serine/threonine phosphatase activity, and is classified as a protein phosphatase 2B (EC 3.1.3.16). It plays an important role in terminating synaptic transmission, and in T-cell activation. It is only weakly inhibited by **okadaic acid**, but potently inhibited by certain pyrethrin compounds. It consists of two subunits, A and B, the A subunit having the catalytic activity and the B subunit conferring calcium sensitivity. Examples, from human, A subunit: database code P2B1_HUMAN, 514 amino acids (58.01 kDa); B subunit: database code CALB_HUMAN, 169 amino acids (19.17 kDa). The B subunit has a myristoylation site at the N terminus.

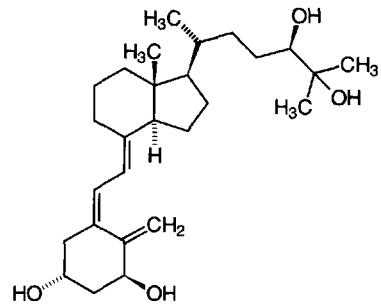
calciol *an alternative trivial name for* **cholecalciferol**.

calciosome a discrete cytoplasmic organelle in non-muscle cells, and a candidate for the inositol 1,4,5-trisphosphate-sensitive Ca^{2+} store. It has a high content of a **calsequestrin**-like protein.

calciotropic describing any hormone or other agonist acting on calcium metabolism.

calciphorin a calcium ionophore polypeptide, M_r 3000, isolated from the inner membrane of calf mitochondria.

calcitetrol *the recommended trivial name for* 1α,24*R*,25-trihydroxycholecalciferol. It is the inactivation product of calcitriol, from which it is formed by calcitriol 24-hydroxylase. *See also* **vitamin D**.



calcitonin *or* **thyrocalcitonin** a 3.4 kDa polypeptide hormone, that regulates the levels of calcium and phosphate in blood. In all species studied it consists of a single polypeptide chain of 32 amino-acid residues with a C-terminal prolinamide residue and an N-terminal seven-membered ring formed by a disulfide bridge between hemicystine residues at positions 1 and 7. The single letter code structure for the polypeptide is

CGNLSTCMLGTYTQDFNKFH-
TFPQTAIGVGAP–NH_2.

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Calcitonin is secreted by the **C cells**, which in mammals occur primarily in the thyroid gland; in more primitive vertebrates they are found mainly in the ultimobranchial bodies and the lung. The hormone is also found to be concentrated in the hypothalamus of humans and some other vertebrates, and in the primitive brain of the chordate organism *Ciona intestinalis*. Calcitonin causes a rapid but short-lived drop in the level of calcium and phosphate in blood by promoting the incorporation of these ions in the bones. Overall its action is antihypercalcemic, opposing that of **parathyrin**. The response of plasma calcitonin to stimulation by administered **pentagastrin** or calcium may be used to screen for medullary cell carcinoma of the thyroid; the level rises to abnormally high values after stimulation, though normal in its absence. The precursor (human example below) and **calcitonin gene-related peptide** precursor are formed by alternative splicing of the same gene: database code CAL0_HUMAN, 141 amino acids (15.45 kDa); calcitonins have three motifs.

calcitonin gene-related peptide *abbr.*: CGRP; a pleiotropic 3.8 kDa polypeptide of 37 amino-acid residues, found in parts of the nervous system and endocrine system, and in some other organs. It is a potent vasodilator and hypotensive agent, and is regarded as a neuromodulatory peptide. The mRNA is formed by **alternative splicing** of the transcript of the **calcitonin** gene, which has exons coding for a region common to both CGRP and calcitonin precursors together with specific calcitonin and CGRP exons. CGRP was the first peptide to be identified by a molecular approach in the absence of biological information; its existence was predicted, in 1983, on the evidence of a second, structurally distinct transcript resulting from calcitonin gene transcription. Initially a 12.5 kDa pro-CGRP is formed, from which a 55-residue 'amino terminal flanking peptide' is generated. The mature polypeptide has the structure (rat)

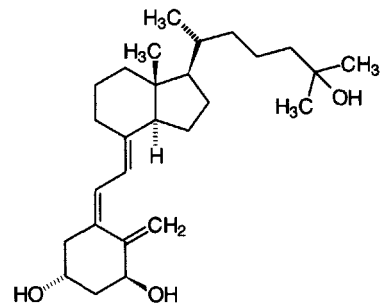
SCNTATCVTHRLAGLLSRSGGVV
KDNFVPTNVGSEAF-NH_2,

a form known as α-CGRP. Another form, known as β-CGRP, is identical except for Lys instead of Glu at position 35, and is encoded by a separate gene related to the calcitonin/CGRP gene but lacking any exon encoding calcitonin. α-CGRP is found in the central nervous system in a distribution distinct from that of any other known neuropeptide; it is present in trigeminal and spinal sensory ganglion cells, in olfactory and gustatory systems, and at neuromuscular junctions. CGRP is also found in the endocrine system – in a subset of adrenal medullary cells and in small amounts in thyroid C cells – in bronchiolar cells, and in intestinal cells. Administration of synthetic rat CGRP causes a drop in blood pressure (CGRP is the most potent known hypotensive gene peptide), and increase in heart rate. *In vitro* it can relax arteries from many vascular beds taken from a variety of species, and is one of the most potent vasodilators known. It also inhibits gastrointestinal motility and causes catecholamine release and gastric hypoacidity. *See also* **amylin**.

calcitonin gene-related peptide receptor any of several membrane proteins that bind calcitonin gene-related peptide (CGRP) and mediate its effects. $CGRP_1$ and $CGRP_2$ subtypes have been proposed; the antagonist $CGRP_{8-37}$ is selective for $CGRP_1$ receptors, and [$Cys(Acm)^{2,7}$]CGRP for $CGRP_2$ receptor types. CGRP receptors are widely distributed in the nervous system, following the pattern of distribution of CGRP, except that receptor numbers are high in cerebellum. They are also widespread in the cardiovascular system, as well as in adrenal, pituitary, exocrine pancreas, kidney, and bone. CGRP receptor stimulation leads to cyclic AMP accumulation in a number of tissues (heart, liver, muscle, pancreatic acinar cells) indicating coupling to one or more G-proteins.

calcitonin receptor any of the membrane proteins that bind calcitonin and mediate its effects. They are seven-transmembrane-helix receptors, normally coupled to G-proteins. In many systems they can activate both adenylate cyclase and the phosphatidylinositol cycle. In some systems, which second messenger system is activated depends entirely on conditions. For example in synchronized cells of a kidney cell line calcitonin activates adenylate cyclase during the G_2 phase, but activates the phosphoinositol cycle during S phase. Activation of the phosphatidylinositol cycle also causes activation of protein kinase C. In other systems, e.g. in brain, adenylate kinase is inhibited, but not through a G-protein. Example (precursor) from human ovarian small cell carcinoma: database code CALT_HUMAN, 490 amino acids (57.3 kDa).

calcitriol *the recommended trivial name for* 1α,25-dihydroxycholecalciferol. *See* **cholecalciferol**, **vitamin D**.



calcium *symbol*: Ca; an alkaline-earth metal of group 2 of the IUPAC **periodic table**; relative atomic mass 40.08, atomic number 20; it occurs naturally only in an ionized (Ca^{2+}) or combined state, and is a mixture of stable nuclides of relative mass 40 (96.97 atom percent) and 44 (2.06 atom percent) with small proportions of nuclides of relative mass 43, 46, and 48. Calcium is the fifth most abundant element of the Earth's crust and is an essential component of all living material. It occurs in bone, shell, and teeth and low concentrations of ionic calcium play many important roles in the regulation of diverse cellular processes. The most abundant mineral in the human body, most of it is in the skeleton. It has especially important functions in bone, in the control of nervous, muscle, and other excitable tissue, and as a **second messenger** and regulator of enzyme activity. Calcium homeostasis depends on the action of: (1) **parathyroid hormone**, which increases tubular reabsorption of calcium, and releases calcium from bone, thereby having overall a hypercalcemic action; (2) **vitamin D** (calcitriol), which causes absorption of calcium from the gut and its release from bone, and also therefore has a hypercalcemic action; and (3) **calcitonin**, which reduces calcium resorption from bone. The range of plasma calcium in normal human adults is 2.2–2.6 mmol L^{-1}. *See also* **hypercalcemia**, **hypocalcemia**.

calcium-45 *symbol*: ^{45}Ca; an artificial radioactive nuclide of calcium, with a half-life of 165 days. It emits β^--particles (i.e. electrons) of 0.252 MeV max. and no γ-radiation.

calcium-47 *symbol*: ^{47}Ca; an artificial radioactive nuclide of calcium, with a half-life of 4.54 days. It emits β^--particles (i.e. electrons) of two energy ranges (1.98 and 0.67 MeV max.) and γ-radiation of three energies (1.31, 0.815, and 0.49 MeV).

calcium channel any of several proteins that permit the controlled (gated) passage of calcium ions through membranes. There are several types. L-type channels are involved in excitation–contraction coupling in muscle; they bind 1,4-dihydropyridine (DHP). The DHP receptor is a protein located in transverse (T-) tubules that specifically binds DHP compounds such as **nifedipine**. This modulates the slow L-type channel in skeletal muscle, neurons, and cardiac cells. N-type channels, identified only in neurons, participate in neurotransmitter release and are blocked by **ω-conotoxin**. T-type channels influence pacemaker activity in the heart and repeti-

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tive spike activity in neurons; they are blocked by octanol. P-type channels, identified in some CNS neurons and prominent in Purkinje cells, are blocked by ω-agatoxin, much less so by ω-conotoxin. The L-type channel from skeletal muscle is hetero-oligomeric, consisting of five subunits: α1, database code CIC1_RABIT, 1873 amino acids (211.78 kDa); α2, database code CIC2_RABIT, 1106 amino acids (124.90 kDa); β, database code CICB_RABIT, 524 amino acids (57.76 kDa); γ, database code CICG_RABIT, 222 amino acids (25.03 kDa); and δ (M_r ≈27 000). The largest subunit (α1) is responsible for many of the functional features, including DHP binding and the voltage-gated pore. It is structurally similar to the Na^+ channel α subunit, with four internal repeats of 200–300 amino acids exhibiting sequence homology. Each of these repeats contains six putative transmembrane segments, S1 to S6; segment S4 in all repeats has positively charged groups in -(K/R)XX- repeats (four to six K or R residues per segment), that have been implicated in sensing voltage changes; potential *N*-glycosylation sites (N residues 79 and 257, rabbit skeletal muscle) and seven potential cAMP-dependent phosphorylation sites (S residues 687, 1502, 1575, 1757, 1772, 1854, T residue 1552) have been identified on the α_1 protein. *See also* **verapamil**.

calcium-dependent regulator protein *or* **calcium-dependent modulator protein** *abbr.*: CDR; *former name for* **calmodulin**.

calcium ion (Ca^{2+})-release channel *another name for* the **ryanodine receptor**.

calcium pump any system that transports calcium ions across a biological membrane from a lower to a higher concentration with the consumption of energy. The term is used especially of the pump in the sarcoplasmic reticulum of muscle of which a transmembrane **calcium-transporting ATPase** is an integral part.

calcium-regulated actin bundling protein a protein that is probably involved in the formation of filopodia. Example from *Dictyostelium discoideum*: database code ACTB_DICDI, 295 amino acids (33.31 kDa).

calcium-transporting ATPase EC 3.6.1.38; an integral membrane protein that forms an essential component of the **calcium pump** in sarcoplasmic reticulum. It catalyses the hydrolysis of ATP to ADP and orthophosphate, simultaneously transporting two calcium ions from the cytosol into the sarcoplasmic reticulum for each ATP hydrolysed. Probably comprising 10 transmembrane domains, it is related to other metal-ion-transporting ATPases. A number of types exist. Example, SR/ER type from *Drosophila melanogaster*: database code ATCB_DROME, 1002 amino acids (109.47 kDa).

calcium-trigger protein any of a group of small calcium-binding **trigger** proteins, including **calmodulin**, troponin C (*see* **troponin**), and **parvalbumin**.

calculus (*pl.* **calculi**) a concretion of material that forms within the body. It often resembles a small pebble, hence is called a 'stone'. Calculi are most common in the gall bladder or kidney, and are composed variously of organic or inorganic salts, frequently of calcium; cholesterol calculi are gallstones of pure cholesterol.

calcyclin *other names*: prolactin receptor associated protein, growth factor-inducible protein 2A9, S100 calcium-binding protein A6; a small protein that copurifies with **prolactin receptor**. It is induced in fibroblasts by growth factors and is overexpressed in acute myeloid leukemia. It binds specifically **annexin** XI. Example from human fibroblasts: database code S106_HUMAN, 90 amino acids (10.18 kDa).

caldecrin a pancreatic protein that lowers serum calcium. It also has chymotrypsin-like activity, which is not needed for the calcium-lowering effect.

caldesmon an F-actin crosslinking protein in thin filaments in smooth muscle and in stress fibres in (nonmuscle) fibroblasts. It also binds myosin and tropomyosin. It appears to be a homodimer comprising two polypeptide chains each with a single actin-binding site and a single self-association site. It controls actin–myosin interactions and inhibits the actin-activated ATPase of myosin. Its action is attenuated by calcium-calmodulin and potentiated by tropomyosin. Caldesmon will interact with Ca^{2+}-calmodulin (but not with calmodulin alone), an interaction that causes caldesmon to dissociate from F-actin. Example from *Gallus gallus*: database code CALD_CHICK, 756 amino acids (86.96 kDa). *See also* **caldesmon kinase**, **caldesmon phosphatase**.

caldesmon kinase EC 2.7.1.120; the name given to a reaction now known to result from the autophosphorylation of **caldesmon** (by ATP) in the presence of calcium. This autophosphorylation abolishes the ability of caldesmon to bind actin.

caldesmon-phosphatase EC 3.1.3.55; an enzyme that hydrolyses the phosphate from caldesmon phosphate.

caldolysin an extracellular protease isolated from *Thermus aquaticus* strain T-351, an extreme thermophile. It contains 13% carbohydrate by weight, and one atom of zinc; M_r 21 000.

calelectrin *see* **annexin IV**, **annexin V**, **annexin VI**.

calgizzarin an **EF-hand** Ca^{2+}-binding protein isolated from chicken gizzard smooth muscle. It is also abundant in rabbit lung and is found in other tissues. It has homology with **annexin** II light chain and is a homodimer (disulfide-linked). It is overexpressed in human colorectal tumours. Example from pig: database code ICAL_PIG, 713 amino acids (77.04 kDa).

callose a linear (1,3)-β-D-glucan insoluble in water but which dissolves in dilute alkali. The glucan chains form stable triple helices. Callose is a ubiquitous higher plant polysaccharide occurring as a component of specialized, and often transient, cell walls, especially in reproductive tissues and is a component of the cell plate. Callose is rapidly deposited on plasma membranes as drops, plugs, or plates on wounding or physiological stress. Callose deposits on cell walls stain specifically with Aniline Blue or its fluorochrome. Specific hydrolases, e.g. glucan endo-1,3-β-D-glucosidase (EC 3.2.1.39) for callose and membrane-bound callose synthetase (EC 2.4.1.34) are found in plants. Functionally callose may act as a temporary wall matrix, as a special permeability barrier or as a wall strengthening agent. Other (1,3)-β-D-glucans include yeast glucan, pachyman, lamarin, scleroglucan, curdlan, leucosin, mycolamarin, paramylon, chrysolamarin, and lentinan.

callus **1** a mass of relatively unspecialized tissue that develops at wound sites in plants, forming a protective covering. Callus cells are used in tissue culture as the starting material for the propagation of plant clones. **2** tissue formed during the healing of broken bone.

calmitine a mitochondrial Ca^{2+}-binding protein of fast-twitch muscle fibres with a characteristic 28-residue signal. The mature protein is identical to **calsequestrin** of the sarcoplasmic reticulum.

calmodulin *abbr.*: CAM; a small, heat-stable, acidic, calcium-dependent modulator protein that binds four calcium ions per molecule and is then able to stimulate a variety of eukaryotic enzymes or enzyme systems. These include brain adenylate cyclase, cytosolic cyclic nucleotide phosphodiesterase, myosin light-chain kinase, erythrocyte Ca^{2+},Mg^{2+}-ATPase, plant NAD^+ kinase, and a number of calcium-dependent protein kinases including phosphorylase kinase (to which it contributes the δ subunits); various other cellular processes such as membrane phosphorylation and microtubule disassembly also are stimulated. Calmodulin consists of a single-chain polypeptide of known sequence, aspartic or glutamic accounting together for about 30% of the total residues; it contains one residue of N^6-trimethyllysine per mole but no cysteine, hydroxyproline, or tryptophan residues. Calmodulin appears to be ubiquitous within the animal and plant kingdoms, to be without species or tissue specificity, and to be almost invariant in structure, being conserved nearly perfectly throughout evolution; it has **EF-hand** domains and is similar to, but not identical with, troponin C from muscle. It was known previously by a variety of provisional names including modulator protein, phosphodiesterase activator protein, troponin C-like (modulator) pro-

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tein, and calcium- (or Ca^{2+})-dependent regulator (or modulator) protein (CDR protein). Examples (1) from black rat: database code NRL_3CLN, 143 amino acids (16.13 kDa); 3-D structure known; (2) from human, rabbit, other rat species, *Xenopus laevis*, chicken, the sea urchin *Arbacia punctulata*, and *Bos taurus*: database code CALM_HUMAN, 148 amino acids (16.13 kDa).

calmodulin-dependent protein kinase II *recommended name*: Ca^{2+}/calmodulin-dependent protein kinase, EC 2.7.1.123; *other names*: Ca^{2+}-CAM kinase II; microtubule-associated protein 2 kinase; multifunctional Ca^{2+}-CAM kinase. An enzyme with broad specificity and activated by Ca^{2+} that catalyses the phosphorylation of Ser and Thr residues in proteins by ATP. It is involved in cell regulation. An oligomeric polypeptide, it is composed of various combinations of α (M_r 60 000) and β (M_r 55 000) subunits in a dodecahedral structure. On activation by Ca^{2+}-CAM, autophosphorylation occurs as a result of which the enzyme converts to a Ca^{2+}-CAM-independent form. Substrates include synapsin I, tryptophan hydroxylase, skeletal muscle glycogen synthetase, and microtubule-associated proteins tau and MAP-2. A synthetic peptide substrate is PLSRTLSVSS. Examples from yeast: type I, database code KCC1_YEAST, 445 amino acids (50.08 kDa); type II (potentially autophosphorylation enzyme), database code KCC2_YEAST, 447 amino acids (50.36 kDa).

calmodulin-like domain protein kinase *abbr.*: CDPK; EC 2.7.1.–; *other name*: Ca^{2+}-binding Ser/Thr protein kinase. An enzyme that is subject to autophosphorylation and resembles calmodulin-dependent protein kinases. Example from soybean: database code CDPK_SOYBN, 508 amino acids (57.10 kDa).

calnexin a calcium-binding protein of the endoplasmic reticulum. It appears to play a role in the processing of endoplasmic reticulum proteins, in monitoring assembly, and in retaining unassembled or incorrectly folded proteins. It has a single transmembrane helical region. Example from human (precursor): database code CALX_HUMAN, 592 amino acids (67.57 kDa); residues 1–20 are the signal, 21–592 calnexin.

calomel electrode the mercury–mercurous chloride (mercury–calomel) ($Hg;Hg_2Cl_2$, Cl^-) half-cell that is reversible to chloride ions. Because of its stability and simplicity, it is frequently used in conjunction with a saturated-KCl bridge as a reference electrode in pH meters, etc.

calorie *or (sometimes)* **gram calorie** *or* **small calorie** *symbol*: cal; any of several units of heat or energy in the CGS system. A calorie originally represented the quantity of heat required to raise one gram of water through one degree centigrade (i.e. Celsius). However, the energy represented by a calorie varies slightly according to the initial temperature of the water. Hence, the **International Table calorie** (*symbol*: cal_{IT}) is now taken to equal 4.1868 J exactly, while the **15 °C calorie** (*symbol*: cal_{15}) is equal approximately to 4.1855 J. Thermochemical calculations have often used a slightly different value; one **thermochemical calorie** (*symbol*: cal_{th}) is now taken to equal 4.184 J exactly. In nutrition and physiology, the term 'calorie' is often used to mean the kilocalorie or Calorie (initial capital), equal to 10^3 cal_{IT}. Use of all these units is now deprecated, the joule now being preferred.

Calorie *or (sometimes)* **kilogram calorie** *or* **large calorie** the name used, especially in nutrition, for the kilocalorie, i.e. 10^3 cal_{IT}. *Compare* **calorie**.

calorific of, relating to, or generating heat.

calorific value the amount of heat produced by the complete combustion of a given mass of a substance, such as a fuel or foodstuff. It is usually expressed in J kg^{-1}.

calorigenesis the production or increased production of heat in an organism. —**calorigenic** *adj.*

calorimeter an instrument for determining quantities of heat evolved, transferred, or absorbed.

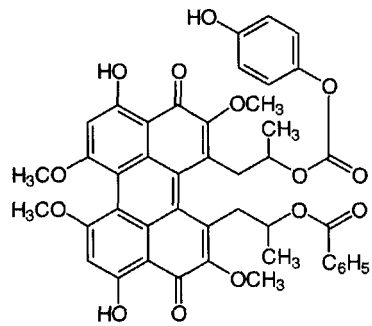
calorimetry the measurement of the amount of heat evolved, transferred, or absorbed by a system. —**calorimetric** *adj.*

calpactin *see* **annexin**.

calpain EC 3.4.22.17; a Ca^{2+}-activated, neutral, thiol proteinase enzyme that preferentially cleaves the bonds: Tyr-|-Xaa, Met-|-Xaa, or Arg-|-Xaa with Leu or Val as the P2 residue. Calpains are cytoplasmic mammalian enzymes, of three main types; these have an identical small regulatory **EF-hand** subunit and large catalytic subunit but differ in their sensitivity to Ca^{2+}. Example (human) calpain II large subunit (responds to millimolar Ca^{2+}): database code CAP2_HUMAN, 700 amino acids (79.92 kDa).

calpastatin a protein, found in liver and erythrocytes of several mammals, that is a specific calpain inhibitor. There are four characteristic domains involved in the inhibitory action. Example (precursor) from pig: database code ICAL_PIG, 713 amino acids (77.04 kDa).

calphostin C one of a group of compounds isolated from *Cladosporium cladosporioides* having a unique structural feature in possessing a perylene quinone. It was identified in a search for inhibition of protein kinases. It inhibits protein kinase C by action on the regulatory domain and has a relatively high degree of specificity, but acts equally on all isoforms having the common regulatory domain. It is a highly potent and specific inhibitor (IC_{50} = 50 nM) of protein kinase C. At higher concentrations it inhibits other kinases, including myosin light chain kinase, and cyclic GMP- and cyclic AMP-dependent kinases.



calphotin a Ca^{2+}-binding protein found in the cytoplasm of photoreceptor cells of *Drosophila melanogaster*. The C-terminal region contains a leucine zipper uninterrupted by prolines. The protein contains >50% proline, alanine, and valine. Database code CPN_DROME, 865 amino acids (84.78 kDa).

calponin a thin filament-associated protein implicated in regulation and modulation of smooth muscle contraction. It is found as an actin-, calmodulin-, and tropomyosin-binding protein present in many vertebrate smooth muscles, and is related to troponin T in immunological and biochemical characteristics. Examples from rat; calponin H1: database code CLP1_RAT, 297 amino acids (33.31 kDa); acidic isoform: database code CLPA_RAT, 330 amino acids (36.39 kDa).

calpromotin a cytoplasmic protein of red cells that activates Ca^{2+}-dependent potassium transport.

calregulin *see* **calreticulin**.

calreticulin *other names*: calregulin; Crp55; CaBP3; HACBP; erp60; a Ca^{2+}-binding protein of the endoplasmic reticulum lumen. Example (precursor) from human: database code CRTC_HUMAN, 417 amino acids (48.09 kDa); amino acids 1–17 constitute the signal; the C terminus contains the **KDEL** sequence.

calsequestrin a 44 kDa calcium-binding protein of low isoelectric point, found on the interior surface of the membrane of the **sarcoplasmic reticulum** of muscle. It acts as an internal calcium store in muscle and releases Ca^{2+} at **calcium channels**. It has only a moderate affinity for calcium ions, but a high ca-

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pacity (>40 Ca^{2+} ions per molecule); selective binding of Ca^{2+} in preference to other cations is promoted by ATP; it also exhibits protein kinase activity. Calsequestrin makes up some 19% of the protein of isolated sarcoplasmic vesicles, and is thought to assist in depleting the sarcoplasm of free calcium ions during relaxation. Example, human muscle isoform: database code CAQS_HUMAN, 390 amino acids (44.53 kDa), very acidic (47 Asp, 56 Glu; has a sequence of eight aspartic-acid residues at the C terminus).

calspectin *an alternative name for* **fodrin**.

calstorin a calcium-binding protein of the microsomal lumen of rat brain, similar to **calsequestrin**.

caltractin *or* **centrin** an **EF-hand** Ca^{2+}-binding protein of the centrosome of interphase and mitotic cells that plays a fundamental role in microtubule-organizing centre structure. It is present in the centrosome/basal body apparatus of the green alga *Chlamydomonas reinhardtii*. It contains four EF-hands, and belongs to the calmodulin/parvalbumin/troponin C superfamily. Example from the salt bush *Atriplex nummularia*: database code CATR_ATRNU, 167 amino acids (19.22 kDa).

caltrin *abbr. for* calcium transport inhibitor; *other name*: seminalplasmin; a small basic protein of male seminal vesicle fluids. It binds to calmodulin and inhibits Ca^{2+} uptake by epididymal spermatozoa. It has antimicrobial properties. Example (precursor, bovine): database code CALT_BOVIN, 80 amino acids (8.97 kDa).

Calvin, Melvin (1911–97), US chemist and biochemist distinguished for pioneering the use of radioactive isotopes, especially carbon-14, as tracers in metabolism; Nobel Laureate in Chemistry (1961) 'for his research on the carbon dioxide assimilation in plants'.

Calvin cycle *see* **reductive pentose phosphate cycle**.

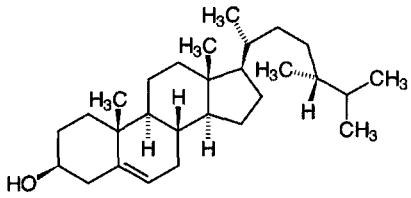
Cam *symbol for* the **carbamoylmethyl** group.

CAM *abbr. for* **1 calmodulin**. **2** crassulacean acid metabolism.

CaM-BP$_{80}$ *an alternative name for* **calcineurin**.

cAMP *abbr. for* cyclic AMP; *see* **adenosine 3′,5′-phosphate**.

campesterol (24*R*)-ergost-5-en-3β-ol; a sterol found in small amounts in rapeseed and other vegetable oils.

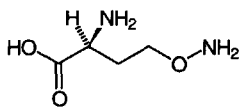


camphor 1,7,7-trimethylbicyclo[2.2.1]heptan-2-one; a compound obtained from the camphor tree, *Cinnamomum camphora*, which is indigenous to Taiwan. It is widely used in ointments and liniments. It is also used as a starting material in organic chemistry.

cAMP receptor protein *see* **catabolite (gene) activator protein**.

cAMP-regulatory protein *see* **catabolite (gene) activator protein**.

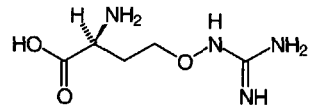
canaline O^4-aminohomoserine; 2-amino-4-(aminooxy)-butanoic acid; $H_2N–O–[CH_2]_2–CH(NH_2)–COOH$; a basic α-amino acid found as the L-enantiomer in the jack bean, *Canavalia ensiformis*, and in some other legumes containing L-canavanine. It is formed from **canavanine** by deamidination or transamidination. It inhibits pyridoxal-dependent enzymes.



canavalin a globular protein isolated from ripe seeds of the jack bean, *Canavalia ensiformis*. It is a storage protein, with sequence similarity to **phaseolin**, **vicilin**, and related proteins. *See also* **concanavalin A**. Example from *Canavalia gladiata*: database code CANA_CANGL, 445 amino acids (50.29 kDa).

canavanase *see* **arginase**.

canavanine O^4-guanidinohomoserine; 2-amino-4-(guanidinooxy) butanoic acid; a basic α-amino acid, occurring as the L-enantiomer in certain legumes esp. the jack bean, *Canavalia ensiformis*; an arginine antagonist. In seeds of the jack bean it constitutes up to 8% of their dry mass and forms their main storage compound for nitrogen. On germination of the seeds the nitrogen is released for synthetic purposes by hydrolysis of L-canavanine to L-canaline and urea, from each of which ammonium is then formed by further hydrolysis. *See also* **canaline**.



cancellate *or* **cancellated** *or* **cancellous** having a porous or spongy structure; meshlike or lattice-like.

cancer any malignant **neoplasm**. Cancers are usually divided into **carcinomas**, derived from epithelial tissue, and **sarcomas**, derived from connective tissue.

cancer-associated retinopathy protein *see* **recoverin**.

candela *symbol*: cd; the SI base unit of **luminous intensity**, defined as the luminous intensity, in a given direction, of a source that emits monochromatic radiation of frequency 540×10^{12} hertz and that has a radiant intensity in that direction of 1/683 watt per steradian.

Candida a genus of (in many cases) dimorphic yeasts containing species of medical (*C. albicans*) and industrial importance: *C. cylindrica* is a source of **lipases** and is a rare example of a eukaryote with a non-standard genetic code for nuclear/cytoplasmic gene expression.

cane sugar *an old and common name for* **sucrose**.

cannabinoid any of about 30 derivatives of 2-(2-isopropyl-5-methylphenyl)-5-pentylresorcinol found in the Indian hemp, *Cannabis sativa*, among which are those responsible for the narcotic actions of the plant and its extracts. The most important cannabinoids are cannabidiol, cannabinol, *trans*-Δ^9-tetrahydrocannabinol, *trans*-Δ^8-tetrahydrocannabinol, and Δ^9-tetrahydrocannabinolic acid. *See also* **cannabis**.

cannabinoid receptor any of several membrane proteins that bind cannabinol and structurally similar compounds and mediate their intracellular action. Two types have been characterized, both of which are seven-transmembrane-domain G-protein-coupled receptors. CB1 receptors are found in brain and testis. CB2 receptors are found in spleen and not in brain. For both types arachidonoylethanolamide (anandamide) is a putative endogenous ligand and both types are negatively coupled to adenylate cyclase decreasing intracellular cyclic AMP levels. Examples from *Mus musculus*: CB1, database code CB1R_MOUSE, 473 amino acids (52.94 kDa); CB2, database code CB2R_MOUSE, 347 amino acids (38.21 kDa).

cannabinol *see* **cannabinoid**.

cannabis the dried flowering or fruiting tops of Indian hemp, *Cannabis sativa*; numerous synonyms exist, including **marijuana**, **bhang**, and **maconha**. A resin, known variously as cannabin, hashish, or charas, is also obtained from the plant. Both preparations contain active principles, **cannabinoids**, and are used as recreational drugs, producing relaxation, euphoria, and enhanced awareness. Occasionally, anxiety or mental disturbance may result, and, rarely, loss of consciousness or even death. The major active ingredients are tetrahydrocannabinols. Cannabis is a controlled substance in the US Code of Federal Regulations.

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Cannizzaro reaction the base-catalysed dismutation of aldehydes with no α hydrogen atoms into the corresponding acids and alcohols:

$$2R\text{–}CHO + OH^- \rightarrow R\text{–}COO^- + R\text{–}CH_2OH.$$

[After Stanislo Canizzaro (1826–1910).]

canonical form *or* **canonical structure** *an older name for* **contributing structure**.

canonical sequence a nucleotide or amino-acid sequence regarded as the archetype with which variants are compared.

cap **1** *or* **cap structure** a structural feature present at the 5′ end of most eukaryotic (cellular or viral) mRNA molecules and also of some virion mRNA molecules but not of bacterial mRNA molecules. It consists of a residue of 7-methylguanosine and a triphosphate bridge linking it 5′–5′ to the end of the polynucleotide chain; in addition, the first one or two nucleotide residues in the chain may possess a 2′-*O*-methyl group and the first, if adenylyl, a 6-*N*-methyl group. The cap structure is thought to protect the 5′ end of the mRNA from degradation by phosphatases or nucleases and to facilitate initiation of translation of mRNA by the eukaryotic (but not by the bacterial) ribosome. **2** a cluster or patch of aggregated proteins at one site on the surface of a cell, e.g. a lymphocyte. Surface components of the cell membrane are aggregated, e.g., by the action of polyvalent ligands, and may be swept to the posterior area of the cell when the cell moves, forming a cap at that site. **3** to form or place a cap on a molecule (or structure).

CAP *abbr. for* **1** catabolite (gene) activator protein. **2** chloramphenicol (use deprecated, full name preferred). **3** *Clostridium* (*histolyticum*) aminopeptidase, EC 3.4.11.13. **4** cyclic AMP receptor protein; *see* **CRP**.

capacitance *or* **electric capacitance** *symbol*: *C*; the ability of a system to store electric charge or a measure of this capacity for a particular system. $C = Q/U$ where Q is the quantity of charge stored to raise the system's potential by U volts. The SI derived unit of capacitance is the **farad**.

capacitance minimization method a simple method for the determination of asymmetric surface potentials in lipid bilayers, based on the dependence of bilayer capacitance on transmembrane voltage. The capacitance is measured by rectifying the 90° component of an applied a.c. current signal. A superimposed slow triangular wave results in a hysteresis-like time course of capacitance. The centre of the hysteresis figure is shifted along the voltage axis by an amount equal to the **capacitance minimization potential**, the difference between the dipole plus surface-charge potentials on the two sides of the membrane.

CAPB *see* **calbindin**.

cap-binding protein any protein (e.g. a 24 kDa protein obtainable from rabbit reticulocytes) that specifically binds to the **cap** (def. 1) of eukaryotic capped mRNA. Such proteins may facilitate the translation of capped mRNA molecules.

CAP factor *see* **catabolite (gene) activator protein**.

capillarity the phenomenon, resulting from surface tension, in which liquids rise up capillary tubes and which also causes them to form a concave or convex meniscus at their surface where it contacts a solid.

capillary **1** of, or relating to, a hair or hairlike structure. **2** of, or relating to, a tube with a very fine bore. **3** any of the very fine blood vessels that form a network between the arterioles and the venules throughout the body. **4** a capillary tube.

capillary column a chromatography column that has a very fine bore (0.1–0.25 mm), the inner surface of which may be coated with **stationary phase** or other support. Such columns are used in gas chromatography, supercritical fluid chromatography, or capillary electrophoresis. The column may be up to a few metres in length, coiled, and made of glass or fused silica. In high-performance liquid chromatography, columns of somewhat wider bore and shorter length are referred to as capillary columns.

capillary electrophoresis *abbr.*: CE; a very-high-resolution method of electrophoresis, also known as **capillary zone electrophoresis** (*abbr.*: CZE) *or* **high-performance electrophoresis**. It is based on the use of long (up to 100 cm), narrow (<100 μm) silica columns for separation of peptides, etc. by electro-osmotic flow. By using sensitive detectors (e.g. laser-induced fluoresence), sensitivity in the attomole range can be achieved.

capillary filtration a technique for **membrane filtration** in which the membrane is supported inside porous capillary tubes (capillary membranes). Bundles of such tubes make up a larger filtration unit. *Compare* **hollow-fibre technique**.

capillary viscometer an instrument for measuring the viscosity of a liquid by determining the rate of flow of the liquid through a capillary tube of known dimensions. An **Ostwald viscometer** is a simple capillary viscometer; an **Ubbelholde viscometer** is a viscometer with several different capillary tubes, so that measurements may be made at different shear values.

capped mRNA an mRNA molecule that has a **cap** (def. 1).

capping the act or process of forming or placing a **cap** on a molecule or structure.

capping enzyme any guanylyltransferase enzyme concerned in the formation of a **cap** (def. 1) on an RNA molecule.

caprate *or* **caprinate** *a trivial name for* **decanoate**, or for any salt or ester of decanoic acid.

capric acid *or* **caprinic acid** *a trivial name for* decanoic acid; *see* **decanoate**.

caprin *a trivial name for* any of the glyceryl esters of decanoic acid (*see* **decanoate**); these often occur in milk fat, especially the triester tricaprin, $(CH_3\text{–}[CH_2]_8\text{–}COO)_3C_3H_5$.

caprinate *see* **caprate**.

caprinyl (*formerly*) *an alternative name for* **caproyl** (def. 1).

caproate *a trivial name for* **hexanoate**, or any salt or ester of hexanoic acid.

caproic acid *a trivial name for* hexanoic acid (*see* **hexanoate**).

caproin *a trivial name for* any of the glyceryl esters of hexanoic acid (*see* **hexanoate**); these often occur in milk fat, especially the triester tricaproin, $(CH_3\text{–}[CH_2]_4\text{–}COO)_3C_3H_5$.

caproyl **1** *or (formerly)* **caprinyl**; *symbol*: Dco; *trivial name for* decanoyl, $CH_3\text{–}[CH_2]_8\text{–}CO\text{–}$, the univalent acyl radical derived from decanoic acid (*formerly* capric acid *or* caprinic acid). Use of the term caproyl is disfavoured because of confusion with **caproyl** (def. 2) and **capryloyl**. **2** *an old trivial name for* hexanoyl, the univalent group derived from hexanoic acid (*formerly* caproic acid), a saturated unbranched, acyclic, aliphatic acid (i.e. fatty acid). It occurs naturally in acylglycerols in, e.g., coconut and palm nut oils, and milk fat. Use abandoned (*see* **caproyl** (def. 1)).

capryl **1** *an old trivial name for* **octyl**. **2** *an old trivial name for sec*-octyl. **3** *symbol*: Dec; *a trivial name sometimes used for* **decyl**.

caprylate *former name for* **octanoate** or for any salt or ester of octanoic acid.

caprylic acid *a former name for* octanoic acid; *see* **capryloyl**.

caprylic alcohol **1** *or* ***n*-caprylic alcohol** *a former name for* (*n*-) octyl alcohol (octan-1-ol). **2** *or* ***sec*-caprylic acid** *a former name for sec*-octyl alcohol (octan-2-ol). *See also* **caprylic acid**.

caprylin *a former name for* any of the glyceryl esters of **octanoic acid**; these occur in milk fat, especially the triester tricaprylin, $(CH_3\text{–}[CH_2]_6\text{–}COO)_3C_3H_5$.

capryloyl *or* **caprylyl** *an old trivial name for* **octanoyl**.

Caps *or* **CAPS** *abbr. for* 3-(cyclohexylamino)propanesulfonic acid; a compound with properties similar to a **Good buffer substance**, pK_a (20 °C) = 10.4.

capsaicin (*E*)-*N*-(4-hydroxy-3-methyoxybenzyl)-8-methylnon-6-enamide; the active principle in chilli pepper (*Capsicum*), paprika, and cayenne that causes a burning sensation by stimulation of nociceptive (pain sensory) neurons followed by desensitization of nociceptive responses and neuronal depletion of **substance P**.

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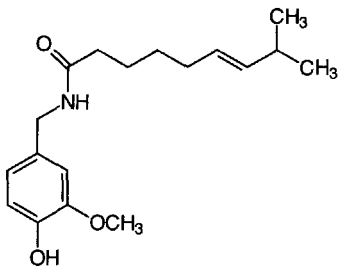


capsaicin

capsanthin (3*R*,3′*S*,5′*R*)-3,3′-dihydroxy-β,κ-caroten-6′-one; the main carotenoid pigment of red pepper (*Capsicum annuum*).

capsid the protein coat that surrounds the infective nucleic acid in some virus particles. It comprises numerous regularly arranged subunits, or **capsomeres**.

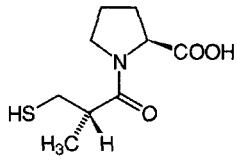
capsomere *or* **capsomer** any of the (protein) subunits that comprise the closed shell or coat (capsid) of certain viruses.

cap structure *see* **cap** (def. 1).

capsular antigen *or* **capsular polysaccharide** *or* **capsular substance** any of the antigens, usually polysaccharide in nature, that are carried on the surface of bacterial capsules. The term **K antigen** is used for those that mask somatic (O) antigens.

capsule **1** an outer layer, rich in polysaccharides, that is present in certain types of bacteria. Presence of a capsule is often linked with **virulence** and the capsular material is often immunogenic. **2** a membrane or sheath of connective tissue that encloses an organ or tissue.

captopril D-3-mercaptomethylpropanoyl-L-proline, (*S*)-1-(3-mercapto-2-methyl-1-oxopropyl)-L-proline; an antihypertensive drug that acts as an inhibitor of **angiotensin converting enzyme**. It was designed to fit the known active site of carboxypeptidase A; the mercapto group binds to the enzyme zinc ion, the amide carbonyl to a hydrogen-bonding site, and the proline carboxylate to an electrophilic centre. A related compound, **enalapril**, is more potent when administered orally and has fewer side effects.



captopril

capture cross-section the probability of a particle that impinges on an atomic nucleus being captured by that nucleus multiplied by the cross-sectional area of the nucleus (measured in **barns**).

carba+ *comb. form (in chemical nomenclature)* indicating the replacement of a heteroatom by a carbon atom.

carbamide *former name for* **urea**.

carbamido *an alternative term for* **ureido**.

carbamino the chemical group –NH–COO^-, which is stable only in the salt form. Carbamino compounds are formed by spontaneous reversible reaction of CO_2 with unprotonated primary aliphatic amino groups; e.g. with α-amino acids to form carbamino acids, or with the N termini of proteins, as in the formation of carbamino hemoglobin from hemoglobin. *Compare* **carbamoyl**.

carbamoyl *or (formerly)* **carbamyl** *or* **carboxamido** *symbol*: Cbm; the acyl group, –CO–NH_2, corresponding to carbamic acid (an acid unknown in the free state). *See also* **carboxamide**.

carbamoylmethyl *symbol*: Cam; the chemical group 2-amino-2-oxoethyl, –CH_2–CO–NH_2.

carbamoyl-phosphate synthase **1** *or* **carbamoyl-phosphate synthase (glutamine-hydrolysing)** EC 6.3.5.5; *other names*: carbamoyl-phosphate synthetase (glutamine-hydrolysing); GD-CPSase. A glutamine-dependent enzyme that is the first step in the pathway for pyrimidine biosynthesis. It catalyses a reaction between 2 ATP, glutamine, CO_2, and H_2O to form 2 ADP, orthophosphate, glutamate, and carbamoyl phosphate; this enzyme is part of the **CAD protein** in many eukaryotes. **2** *or* carbamoyl-phosphate synthase (ammonia) EC 6.3.4.16; *other names*: carbamoyl-phosphate synthetase (ammonia); carbamoyl-phosphate synthetase I, carbon-dioxide–ammonia ligase. An enzyme that incorporates free ammonium ion into carbamoyl phosphate, which then enters the **ornithine–urea cycle**. It catalyses a reaction between 2 ATP, NH_3, CO_2, and H_2O to form 2 ADP, orthophosphate, and carbamoyl phosphate. Example of latter type from human mitochondria: database code CPSM_HUMAN, 1500 amino acids (164.64 kDa).

carbamyl *former name for* **carbamoyl**.

carbanion any anion containing an even number of electrons in which a significant part of the excess negative charge is located on one or more carbon atoms.

carbapenem antibiotic any of various broad-spectrum β-lactam antibiotics, such as thienamycin derived from *Streptomyces cattleya*, that inhibit peptidoglycan synthesis. Semisynthetic derivatives include imipenem.

carbene **1** any chemical species of the type R_2C: containing an electrically neutral, bivalent carbon atom with two nonbonding electrons. The spins of such electrons may be either antiparallel (in the singlet state) or parallel (in the triplet state). Carbenes are highly reactive short-lived groups formed as intermediates in the course of certain organic reactions. **2** *or (formerly)* **methylene** the chemical group H_2C:, the simplest of the carbenes.

carbenium ion any real or hypothetical **carbocation** with one important contributing structure containing a tervalent carbon with a vacant *p*-orbital. These structures have often been described as **carbonium ions**.

carbenoxolone glycyrrhetic acid hydrogen succinate, a 3-(3-carboxy-1-oxopropoxy)-11-oxoolean-12-en-29-oic acid, steroid agent with anti-ulcerative effects, the mechanism of which is unresolved.

carbobenzyloxy *or* **carbobenoxy** *former name for* **benzyloxycarbonyl**.

carbocation a cation with an even number of electrons with a significant portion of the excess positive charge located on one or more carbons. This general term includes **carbenium ions**, **carbonium ions**, etc.

carbocycle any compound or molecular structure that is **carbocyclic** (def. 1); a **carbocyclic** (def. 2).

carbocyclic **1** describing any cyclic molecular structure containing only carbon atoms in the ring or rings; describing any compound having such a stucture. *See also* **homocyclic** (def. 1). *Compare* **heterocyclic** (def. 1). **2** *or* **carbocycle** any such compound.

carbodiimide any organic compound of general structure R–N=C=N–R, widely used for forming amide (peptide) or phosphodiester linkages in the laboratory. Water-soluble carbodiimides, e.g. 1-ethyl-3-(3-dimethylaminopropyl)carbodiimide, are used to couple carboxylic acid residues to ω-aminoalkyl agarose, while for reactions in nonaqueous media *N*,*N*′-dicyclohexylcarbodiimide is much used.

carbohydrase *former name for* **glycosidase**.

carbohydrate any of a group of organic compounds based on

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the general formula $C_x(H_2O)_y$. The group comprises the **monosaccharides**, **oligosaccharides**, and **polysaccharides**, and is usually extended to include their derivatives and, sometimes, the **cyclitols**. Some of the simplest members of the group may, notionally, be considered as hydrates of carbon. However, note that the very important carbohydrate, 2-deoxy-D-ribose ($C_5H_{10}O_4$), does not fit the empirical formulation.

carbon *symbol*: C; a nonmetallic element of group 14 of the IUPAC **periodic table**; atomic number 6; relative atomic mass 12.011. It exists in two main allotropic forms, diamond and graphite, and as a third allotrope, fullerene; there are also several amorphous forms, such as carbon black and charcoal. Carbon also forms a vast array of compounds, the organic compounds, based on chains and rings of covalently bonded carbon atoms. There are two stable nuclides, the predominant one being carbon-12. This has a relative abundance in natural carbon of 98.89 atom percent. Its mass is used as the reference standard for all relative atomic masses of nuclides. The other stable nuclide is **carbon-13**. There are also four radioactive nuclides: carbon-10, **carbon-11**, **carbon-14**, and carbon-15.

carbon-11 a radioactive nuclide of carbon, $^{11}_{6}C$. It emits a positron (β^+-particle) (0.97 Mev), no γ-ray, and has a half-life of 20.3 min.

carbon-13 *or* **heavy carbon** the stable nuclide $^{13}_{6}C$. Relative abundance in natural carbon 1.108 atom percent. It is used as a tracer in studies of reaction mechanisms and of carbon metabolism; now often replaced by **carbon-14** unless double labelling is required. Carbon-13 was/is used when a non-radioactive isotope is essential. *See also* **carbon-13 nuclear magnetic resonance spectroscopy**.

carbon-14 a radioactive nuclide of carbon, $^{14}_{6}C$. It emits an electron (β^--particle) (0.156 Mev), no γ-radiation, and has a half-life of 5730 years, decaying to $^{14}_{7}N$. A minute proportion occurs in atmospheric CO_2 due to the action of cosmic rays, and it forms the basis of **carbon dating**. It is used very widely as a radioactive tracer, for which it is produced artificially.

carbonate dehydratase EC 4.2.1.1; *systematic name*: carbonate hydro-lyase; *other names*: carbonic dehydratase; carbonic anhydrase; an enzyme that catalyses the reversible hydration of carbon dioxide to carbonic acid (or to bicarbonate ion at certain pH values) in a wide range of species. Zinc is a cofactor. It is an intracellular enzyme, present in erythrocytes, and is needed to accelerate the reaction, which, although it occurs spontaneously, would not be sufficiently rapid for the needs of higher animals. CO_2 entering the blood from tissues is taken up by the erythrocytes and released as bicarbonate. At least seven enzymatic forms are known, designated carbonic anhydrases I to VII (*abbr.*: CA-I to CA-VII). Example of CA-I from *Chlamydomonas reinhardtii* (precursor): database code CAH1_CHLRE, 377 amino acids (41.63 kDa). Example from human (type I): database code CAH1_HUMAN, 260 amino acids (28.71 kDa). *See also* **dehydratase**.

carbon cycle the sum total of chemical and biochemical processes whereby carbon is cycled between carbon dioxide in the atmosphere (and oceans) and organic compounds in organisms and their remains. Atmospheric carbon dioxide is fixed during photosynthesis by green plants and other photoautotrophic organisms, using solar energy to split water molecules and liberate O_2. The carbon dioxide is thus converted into glucose and other organic compounds, which are used as metabolic fuel and building blocks by the majority of organisms. Aerobic organisms, in particular, are able fully to oxidize organic compounds during respiration to release carbon dioxide to the atmosphere. The carbon stored in the remains of dead organisms is liberated by the respiration of decomposers or, especially that in fossil fuels, by combustion. Hence, photosynthetic organisms and aerobic heterotrophic organisms exist in a state of syntrophy. However, green plants and other aerobic autotrophs also liberate carbon dioxide during respiration. *Compare* **oxygen cycle**.

carbon dating *or* **radiocarbon dating** a technique for determining the age of specimens of biological origin, e.g. wood. It is based on determining the amount of **carbon-14** remaining in the specimen, the known half-life of carbon-14, and the assumption that the abundance of this radionuclide in the atmosphere has remained constant since its incorporation into the material from atmospheric CO_2.

carbon-dioxide buffer any aqueous solution of a water-soluble salt, pK_a 9–10, that, when equilibrated with CO_2, is capable of maintaining a constant partial pressure of CO_2 (pCO_2) in the gas phase in a closed vessel. Carbon-dioxide buffers are used especially in maintaining a constant pCO_2 in manometric experiments on reactions involving the steady production of that gas.

carbon-dioxide electrode an electrode system for determining CO_2 tension in a gas or a liquid. It consists of a combination pH electrode bathed in a thin layer of a dilute bicarbonate solution, the whole being separated from the sample by a rubber or silicone-rubber membrane permeable to CO_2 but not to water or ionizable solutes. The pH of the layer of bicarbonate solution, and hence the electrode's response, varies logarithmically with the CO_2 tension in the sample.

carbon-dioxide fixation the process whereby the carbon atoms of carbon dioxide are incorporated into hexoses by the **reductive pentose phosphate cycle**.

carbon-dioxide snow solid carbon dioxide in powder form. *See also* **dry ice**.

carbonic anhydrase *common name for* **carbonate dehydratase**.

carbonium ion any real or hypothetical cation, containing an even number of electrons and at least one penta-coordinate carbon atom, in which a significant part of the excess positive charge is located on one or more carbon atoms. *See also* **carbenium ion**, **carbocation**.

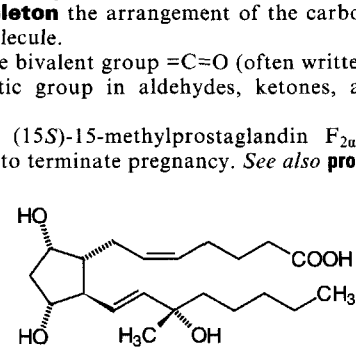
carbon monoxide CO; a colourless, odourless, toxic gas that combines with hemoglobin to form **carboxyhemoglobin**; it also combines with and inhibits cytochrome oxidase. In very small amounts it functions as a neurotransmitter.

carbon-13 nuclear magnetic resonance spectroscopy *or* **^{13}C-NMR spectroscopy** a variant of **nuclear magnetic resonance spectroscopy** in which resonances in **carbon-13** nuclei in natural carbon of organic molecules are examined instead of proton responses. Carbon-12 has no NMR spectrum, and with a natural abundance of carbon-13 of 1.11%, a carbon-13 NMR spectrum has a several thousandfold disadvantage in signal-to-noise ratio compared with a proton NMR spectrum. However, the carbon-13 spectrum is much simpler and therefore has a particular advantage in large molecules. Since ^{13}C–^{13}C coupling can be observed, a double labelling tracer technique is possible, using e.g. $^{13}CH_3$–$^{13}COOH$ as a precursor in studies of **polyketide** biosynthesis.

carbon skeleton the arrangement of the carbon atoms in an organic molecule.

carbonyl the bivalent group =C=O (often written =CO); it is a characteristic group in aldehydes, ketones, and carboxylic acids.

carboprost (15*S*)-15-methylprostaglandin $F_{2\alpha}$; an oxytocic agent used to terminate pregnancy. *See also* **prostaglandins**.



Carbowax *proprietary name for* a group of polyethylene glycols of general formula $H[OCH_2–CH_2]_n–OH$ and of average M_r 400 to 20 000.

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carboxamide an amide derived from a carboxylic acid. The carboxamide group is $-CO-NH_2$. *See also* **carbamoyl**.

carboxamido *former name for* **carbamoyl**.

carboxy+ *prefix (in chemical nomenclature)* denoting the presence of a carboxyl group.

carboxyethyl *symbol*: Cet; the $-CH_2-CH_2-COOH$ group.

4-carboxyglutamic acid *or* **γ-carboxyglutamic acid** *symbol*: Gla; 1-aminopropane-1,3,3-tricarboxylic acid; a **noncoded amino acid**, one or more residues of which are present in a number of calcium-binding proteins, e.g. **osteocalcin** and **blood coagulation** factors II, VII, IX, and X. It is formed subsequent to biosynthesis of the proteins by vitamin K-dependent carboxylation of glutamic acid residues.

carboxyhemoglobin a form of hemoglobin in which carbon monoxide has displaced oxygen from the heme group of hemoglobin, to which it binds with much greater affinity and thus less reversibly than oxygen. The formation of carboxyhemoglobin thus reduces the oxygen-carrying capacity of the blood and deprives tissues of oxygen. It is the basis of carbon monoxide poisoning.

carboxyl the chemical group –COOH in an organic molecule; it is acidic in character.

carboxylate **1** the anionic group $-COO^-$, formed by dissociation of a **carboxyl** group. **2** any salt, anion, or ester formed from a **carboxylic acid**. **3** to perform or undergo **carboxylation**.

carboxylation the introduction of a molecule of CO_2 into an organic compound.

carboxylic acid any organic acid containing one or more carboxyl (–COOH) groups.

carboxyl protease *see* **aspartic proteinase**.

carboxyl proteinase *or* **acid proteinase** *or* **aspartic proteinase** any enzyme of the sub-subclass EC 3.4.23 (aspartic endopeptidases), a common feature of which is a low pH optimum and an aspartic acid residue in the active centre. It includes **pepsins**, **rennins**, and **cathepsin D**.

carboxyl terminus *or* **carboxyl terminal** *an alternative name for* the **C terminus** of a polypeptide chain (also called, less correctly, carboxy terminus or carboxy terminal). —**carboxy-terminal** *adj.*

carboxy-lyase any enzyme of sub-subclass EC 4.1.1 that catalyses a decarboxylation reaction.

carboxymethyl *symbol*: Cm; the $-CH_2-COOH$ group.

carboxymethylation the process of introducing **carboxymethyl** groups into a substance; e.g. cellulose may be carboxymethylated to produce a cation-exchanger.

carboxypeptidase any enzyme of the sub-subclasses serine carboxypeptidases (EC 3.4.16) or metallo-carboxypeptidases (EC 3.4.17). Both types hydrolyse C-terminal amino-acid residues from oligopeptides or polypeptides. *See* **carboxypeptidase A**, **carboxypeptidase B**, **carboxypeptidase H**.

carboxypeptidase A EC 3.4.17.1; *other name*: carboxypolypeptidase. A **carboxypeptidase** enzyme that catalyses the hydrolysis of peptidyl-L-amino acid to peptide and L-amino acid; zinc is a cofactor.

carboxypeptidase B EC 3.4.17.2; *other name*: protaminase. A **carboxypeptidase** enzyme that catalyses the hydrolysis of peptidyl-L-lysine (or L-arginine) to peptide and L-lysine (or L-arginine); zinc is a cofactor.

carboxypeptidase E *see* **carboxypeptidase H**.

carboxypeptidase H EC 3.4.17.10; *other names*: carboxypeptidase E; enkephalin convertase; *(wrongly)* enkephalinase. A **carboxypeptidase** enzyme involved in prohormone processing. It catalyses the hydrolysis of peptidyl-L-lysine (or L-arginine) to peptide and L-lysine (or L-arginine); zinc is a cofactor. Example from human: database code CBPH_HUMAN, 476 amino acids (53.09 kDa).

carboxypeptidase-tubulin *see* **tubulinyl-Tyr carboxypeptidase**.

carboxy-terminal *see* **carboxyl terminus**.

carboxy terminus *a less correct alternative term for the* **C terminus** of a polypeptide chain. *See also* **carboxyl terminus**.

carcinoembryonic antigen *abbr.*: CEA; any member of a subfamily of immunoglobulin-like proteins on the outer cell surface and grouped in the cluster CD66 (*see* **CD markers**). **CD66e**, *other name*: **meconium antigen 100**, mass 180–200 kDa, was first found in extracts of tumour tissue and of normal fetal colon. It is a glycoprotein, attached to the membrane by a GPI-anchor. It is present in elevated concentrations in many patients with colorectal cancer, but its presence is too variable in this and other diseases for screening for the condition. However, it can be used for monitoring therapy. Example, human (precursor): database code CCEM_HUMAN, 702 amino acids (76.8 kDa). **CD66d**, *other names*: **CGM1**, **CEA gene member 1**, is present on leukocytes and granulocytes, but not lymphocytes, monocytes, or tumours. Several forms are produced by alternative splicing. Example, human (precursor): database code CGM1_HUMAN, 252 amino acids (27.08 kDa). **CD66b** (*formerly* CD67), *other names*: **CGM6**, **CEA gene member 6**, is expressed in leukocytes of chronic myeloid leukemia patients and bone marrow. It is attached to the membrane by a GPI-anchor. Example, human (precursor): database code CGM6_HUMAN, 349 amino acids (38.13 kDa).

carcinogen any agent that directly or indirectly induces the transformation of a normal cell into a neoplastic cell. Such agents include various substances of small M_r (often termed **chemical carcinogens**), **oncogenic** viruses, ionizing radiations, and ultraviolet light. *See also* **precarcinogen**, **proximate carcinogen**. —**carcinogenic** *adj.*

carcinogenesis the process(es) involved in the production of **cancers**, including the action of **carcinogens** on living cells. *See also* **oncogenesis**.

carcinogenicity the measure or extent of the potency of a chemical **carcinogen**.

carcinoid (tumour) *or* **argentaffin carcinoma** *or* **argentaffinoma** any tumour arising from **argentaffin cells**. Carcinoids arise from any site of such cells, notably in the ileocecal region, and produce large amounts of 5-hydroxytryptophan and 5-hydroxytryptamine, the former mainly by bronchial tumours and the latter by the decarboxylase-containing intestinal tumours. Histamine, kinins, and substance P may also be produced.

carcinoma any cancer that arises from epithelial tissue. Carcinomas form malignant tumours that tend to invade lymph spaces in surrounding connective tissue and to spread by lymphatic permeation and embolism; they also enter the bloodstream to form **metastases**. —**carcinomatous** *adj.*

cardenolide any of a group of C_{23} cardiotonic steroids characterized by a 14β-hydroxyl group and an unsaturated γ-lactone ring on C-17. They occur free or as the aglycons of **cardiac glycosides** in plants and insects.

cardiac **1** of, relating to, or affecting the heart. **2** of, or relating to, the upper part of the stomach.

cardiac glycoside any of a group of toxic steroid glycosides, derived from plants, that in pharmacological doses increase the power of the contractions of the mammalian heart; some are inhibitors of Na^+,K^+-ATPase. The steroid aglycon carries a 17β unsaturated pentenyl lactone ring and a 3β-hydroxyl group to which the carbohydrate moiety is attached. Examples are **digitoxin** from *Digitalis purpurea*, **ouabain** from *Strophanthus gratus*, and **strophanthin** from *Strophanthus kombe*.

cardiac muscle the specialized muscle of which the walls of the vertebrate heart are made. It is composed of a network (syncytium) of branching elongated cells (fibres) with cross striations, and undergoes spontaneous rhythmical contractions.

cardiac puncture a convenient and quick method for obtaining reasonable volumes of blood from an animal by inserting a syringe needle directly into the heart.

Cardice *proprietary name for* solid carbon dioxide. *See* **dry ice**.

cardio+ *or (before a vowel)* **cardi+** *comb. form* denoting heart.

cardioid *(in mathematics)* a type of expression that yields a heart-shaped curve.

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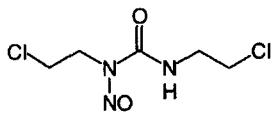
cardiolipin an immunogenic 1,3-bis(3-phosphatidyl)glycerol, extracted from beef heart, that is used as an active antigen in the **Wassermann reaction** and other serological tests for syphilis. It may carry antigenic determinants similar to *Treponema pallidum* or be similar to products of tissue necrosis formed when the spirochaete attacks human tissues.

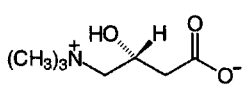
cardiotonic having the effect of improving the tone of heart muscle. Cardiotonic steroids (**cardiac glycosides**) act directly on heart muscle to restore the power of the heart's contractions.

cardiovascular of, or relating to, the heart and the system of blood vessels.

carmustine 1,3-bis(2-chloroethyl)-1-nitrosourea; an antineoplastic derivative of chloroethylnitrosourea with immunosuppressive and antifungal activity.



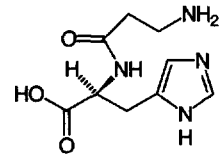
carnitine γ-amino-β-hydroxybutyric acid trimethylbetaine, 3-carboxy-2-hydroxy-*N*,*N*,*N*-trimethyl-1-propanaminium hydroxide, inner salt; $(CH_3)_3N^+–CH_2–CH(OH)–CH_2–COO^-$; a compound that is found in striated muscle, liver, and other tissues and participates in the transfer of acyl groups across the inner mitochondrial membrane. **Carnitine acyltransferases** catalyse the transfer of acyl groups to and from acyl-CoA molecules to form *O*-acylcarnitine, which can exchange across the inner mitochondrial membrane with unacylated carnitine. This cyclic movement of carnitine is sometimes referred to as the **carnitine shuttle**.



L-carnitine

carnitine acyltransferase *or (sometimes)* **carnitine acylase**. any of various enzymes that catalyse a reaction between acyl-CoA and carnitine to form CoA and *O*-acylcarnitine. **Carnitine *O*-acetyl transferase**, EC 2.3.1.7, is a soluble enzyme found (in eukaryotes) in the mitochondrial matrix, peroxisomes, and the lumen of the endoplasmic reticulum. It is specific for short-chain fatty acyl-CoA (C_2–C_{14}), having no activity with palmitoyl-CoA. In transferring acyl groups to carnitine, it maintains the concentration of free coenzyme A, and also provides a mechanism for the transport of acetyl groups, as acetylcarnitine, through the mitochondrial membrane. Example from yeast: database code CACP_YEAST, 670 amino acids (77.19 kDa). **Mitochondrial carnitine palmitoyltransferase**, EC 2.3.1.21, exists as two isoforms. One isoform, CPT_1 *or* CPT-I, is a mitochondrial outer membrane protein involved in regulating fatty acid β-oxidation by controlling the rate of formation of carnitine acyl esters; database code CPT1_RAT, 773 amino acids (88.04 kDa); another isoform, CPT_2 *or* CPT-II, is located in the mitochondrial inner membrane and reforms acyl-CoA esters in the mitochondrial matrix after the carnitine esters have been transported through the inner membrane by acylcarnitine:carnitine antiporter.

carnosine *N*-β-alanyl-L-histidine; a substance that occurs in the skeletal muscle of some animals, including humans (up to 30 mmol kg^{-1}). *Compare* **anserine**.



carnosine

carotene *see* **carotenoid**.

carotenoid any of a group of naturally occurring tetraterpenes that are widely distributed in plants and animals but only synthesized by higher plants, algae, fungi, and bacteria. They may be represented formally as consisting of eight isoprenoid (ip) residues and formed by the joining tail to tail of two units each comprising four ip residues joined head to tail: ip.ip.ip.ip.pi.pi.pi.pi. There are two groups of carotenoids: **carotenes**, which are hydrocarbons, and **xanthophylls**, which contain oxygen in various forms. They occur in all photosynthetic tissues, where they function as protectors against photosensitization and as antenna pigments in photosynthesis.

carrageenan *or* **carrageen** *or* **carrageenin** a mixture of sulfated galactans, also known as **Irish moss**, extracted from red seaweeds (class Rhodophyceae), particularly *Chondrus crispus* and *Gigartina stellata*. It shows blood anticoagulant activity and is used as a gelling and stabilizing agent in foods and pharmaceuticals. Three major types are known: ι-carrageenan is the most highly sulfated and contains alternate units of 3-linked β-D-galactopyranose 4-sulfate and 4-linked 3,6-anhydro-α-D-galactopyranose 2-sulfate; κ-carrageenan is precipitated by potassium chloride and contains only one sulfate per disaccharide unit; λ-carrageenan is largely devoid of the 3,6-anhydro component. ι-Carrageenan forms a kinked double-helical structure. [After Carragheen, near Waterford, Republic of Ireland.]

κ-carrageenase EC 3.2.1.83; an enzyme that catalyses the hydrolysis of 1,4-β-D-linkages between D-galactose 4-sulfate and 3,6-anhydro-D-galactose in various carrageenans.

carrier **1** any known or putative component of a biological membrane that effects the transfer of a specific substance or group of related substances from one side of the membrane to the other. The mechanism is supposedly a cyclic process, involving combination of the carrier with the substance(s) on one side of the membrane, diffusion of the combined form across the membrane, release of the substance(s) on the far side, and diffusion of the carrier back across the membrane in uncombined form. *See also* **facilitated diffusion**, **permease**, **translocation**, **transport**. **2** any component of a biological fluid (e.g. a blood protein) that can combine with a specific substance (e.g. a hormone or metabolite) and transport it from one part of the organism to another. **3** *(in enzymology)* any substance undergoing reversible combination with a metabolite or reversible oxidation–reduction and thereby carrying the metabolite, electron(s), or hydrogen atom(s) between enzymes or cellular organelles, or into cells. Some **coenzymes** may act as carriers. *See* **electron carrier**, **hydrogen carrier**. **4** a substance that is mixed with a reagent or other substance to facilitate the chemical or physical manipulation of the latter. The carrier is commonly of similar constitution and/or properties to the reagent, and present at relatively high concentration. The term is used especially for the nonradioactive chemical counterpart of a radionuclide or of a compound containing a radionuclide, whether deliberately added or present from the time of initial preparation of the radioactive substance. *Compare* **carrier-free**. **5** *(in chromatography)* the **mobile phase** or a component thereof. *See* **carrier ampholyte**, **carrier displacement chromatography**, **carrier gas**. **6** *or* **matrix** the inert support material to which a small molecule, biopolymer, cell fragment, or intact

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cell is artificially linked to form an immobilized or insolubilized derivative. *See also* **microcarrier**. **7** any vesiculated structure within which a biologically active substance (e.g. a drug or enzyme) is artificially incorporated, commonly to protect the substance from degradation and/or to direct it to a target organ upon injection into the bloodstream. Such a carrier may be either artificial (e.g. a **liposome**) or of natural origin (e.g. an erythrocyte **ghost**). **8** *(in immunochemistry)* any substance of high M_r (e.g. a protein) to which a non- or poorly immunogenic substance (e.g. a **hapten**) is naturally or artificially linked to enhance its immunogenicity. **9** *(in genetics)* any individual who is heterozygous for a specified recessive allele and who thus does not normally display any characteristic (e.g. a disease) associated with that allele but who may, with appropriate mating, produce homozygous offspring that exhibit the recessive characteristic. **10** *(in pathology)* any individual who harbours a specified infectious microorganism without showing signs of disease, and is capable of transmitting the microorganism to others. *Compare* **vector** (def. 2). *See also* **vehicle**.

carrier ampholyte a mixture of amphoteric electrolytes used in **isoelectric focusing** to generate a linear and stable pH gradient, and in **isotachophoresis** and **ampholyte displacement chromatography**. The component electrolytes are commonly of similar constitution, low molecular mass, and closely spaced isoelectric points. *See also* **Ampholine**.

carrier displacement chromatography a variant of **displacement chromatography** in which substance(s), either related or unrelated, are added to the mixture being chromatographed to assist in the manipulation of the components separated.

carrier-free describing a preparation of a radionuclide, or of a radionuclide-labelled compound, to which no carrier has been added, and for which precautions have been taken to minimize contamination with other isotopic nuclides. It does not necessarily imply, however, 100% isotopic abundance. Material of high specific activity is often wrongly referred to as 'carrier-free'; more correctly it would be of high isotope abundance.

carrier gas the inert gas that forms the mobile phase in **gas–liquid chromatography** or gas–solid chromatography and that carries the eluted substances in gaseous form into the detector.

carrier lipid *see* **undecaprenol**.

carrier protein any protein that functions as a **carrier** (def. 8), e.g. **acyl carrier protein**. The term has been applied more specifically to describe **cytochome b_5**, ADP,ATP carrier protein, and **GDC** (Graves' disease carrier protein).

Carr-Price reaction the reaction of an anhydrous solution of antimony trichloride in chloroform with retinol (vitamin A) to produce a transient blue colour, maximal at about 10 s. It can be used to estimate retinol.

CARS *abbr. for* **coherent anti-Stokes Raman spectroscopy**.

Cartesian of, or relating to, **Descartes** or his works.

Cartesian coordinates a system of coordinates that defines the location of a point in a plane (two dimensions) or in a space (three dimensions) in terms of its perpendicular distance from each of a set (two or three) of mutually perpendicular axes.

Cartesian diver *or* **Cartesian devil** a device, devised as a toy, adapted as an ultramicrorespirometer, consisting of a small piece of capillary glass tubing open at one end and closed and slightly expanded at the other. A sample of tissue, in approximately 2 μL buffer, is placed in the vessel which is then filled with gas and the neck sealed with a drop of oil. The diver is placed in a constant-temperature vessel filled with a solution in which the diver just floats. If the pressure in the vessel is reduced the diver will rise and if the pressure is increased the diver will fall. The buoyancy of the diver is determined by the gas volume within it, and changes in the latter may be measured by adjusting the pressure in the vessel so that the diver floats in the same position.

cartilage a tough, elastic type of **connective tissue**, found in most vertebrates. It is a major component of the embryonic skeleton, but in higher vertebrates it is mostly converted to bone during development. In adult humans, it is largely confined to the ears, nose, trachea, the anterior ends of the ribs, and the articular surfaces of bones. Cartilage consists of a firm resilient matrix, formed by chondroblasts (which become enclosed as chondrocytes), and composed of glycosaminoglycans including **chondroitin sulfate** A and C, hyaluronic acid, and keratosulfate II, together with varying amounts of **collagen**. The entire skeleton of some lower vertebrates, notably the cartilaginous fishes (class Chondrichthyes), consists of cartilage. —**cartilaginous** *adj.*

cartilage link protein a protein that stabilizes the aggregates of proteoglycan monomers with hyaluronic acid in the extracellular cartilage matrix. Example (precursor) from human: database code PLK_HUMAN, 354 amino acids (40.12 kDa).

cartilage oligomeric matrix protein *abbr.*: COMP; a pentameric disulfide-linked Ca^{2+}-binding **EF-hand** protein of the cartilage matrix. Example (precursor) from *Rattus norvegicus*: database code COMP_RAT, 755 amino acids (82.57 kDa).

cartilage-specific proteoglycan core protein a major proteoglycan of the extracellular matrix of cartilaginous tissues. The N-terminal region binds hyaluronic acid. Chondroitin sulfate is the main glycan component, but keratan sulfate and O-linked and N-linked oligosaccharides are also present. It also has an epidermal growth factor-like domain and a **Sushi domain**. Example (precursor) from human: database code PGCA_HUMAN, 2415 amino acids (250.19 kDa).

caryon *a variant spelling of* **karyon**.

caryopsis *see* **grain**.

CAS *abbr. for* carbonic anhydrase.

cascade sequence *or* **waterfall sequence** a sequence of successive activation reactions involving either enzymes (**enzyme cascade**) or hormones (**hormone cascade**), or both. There are various examples: (1) the series of transformations of proteolytic enzymes in **blood coagulation** in which each enzyme activates the next until the final substrate, fibrinogen, is reached; (2) the series of reactions involved in the formation of, and mediation of the action of second messengers, e.g. in the activation of **glycogen phosphorylase**; (3) the process of activation of **steroidogenesis** in the adrenal gland by hypothalamic and pituitary hormones. The term has also been applied to other sequential phenomena, e.g. DNA → RNA → protein. Cascade sequences are characterized by a series of amplifications of a weak initial stimulus, and may be activated at more than one point along the sequence.

cascara the dried bark of the small tree *Rhamnus purshiana*. It is a potent purgative due to its constituent hydroxyanthracene derivatives (anthroglycosides), including cascarosides and related glycosides. These yield active anthracene derivatives after metabolism by colonic bacteria.

casein **1** *or (esp. Brit.)* **caseinogen** the principal protein fraction of milk; it is present as a colloidal suspension and may be precipitated by acidification. It is a mixture of several related proteins – α-, β-, γ-, and κ-caseins – which differ in amino-acid composition and which may be separated electrophoretically. The α- and β-caseins are rich in phosphate, present mainly as *O*-phosphoserine residues, which bind calcium ions. Casein is easily prepared and is valuable as a dietary supplement. **2** *or (esp. US)* **paracasein** the product formed by coagulation of milk (or **casein** (def. 1)) by treatment with chymosin (rennin). This enzyme removes a 64-residue carbohydrate-rich hydrophilic C-terminal moiety of κ-casein, thereby destroying the latter's protective action on the casein micelles and thus allowing them to be precipitated by the calcium ions present. Examples from *Bos taurus*, β-casein (precursor): database code CASB_BOVIN, 224 amino acids (25.11 kDa); κ-casein (precursor): database code CASK_BOVIN, 190 amino acids (21.27 kDa).

caseinogen *an alternative name (esp. Brit.) for* **casein** (def. 1).

casomorphin *or* **exomorphin** any of a number of opioid peptides isolated from an enzymatic digest of bovine casein; activ-

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ity corresponds to residues 60–66 of bovine β-casein. *See also* **morphiceptin**.

caspase *see* **apoptosis**.

castor oil an oil derived from seeds of the plant *Ricinus communis*. It contains triglycerides of ricinoleic, oleic, linoleic, palmitic, and stearic acids.

CAT *abbr. for* **1** computer of average transients. **2** chloramphenicol *O*-acetyltransferase. **3** computer-assisted tomography.

catabolic dead-end a point in a **catabolic pathway** where, in a particular organism, a metabolite is neither catabolized further nor excreted but accumulates intracellularly. Consequently the pathway is unable to function as an energy-yielding process. The enzyme that can form the metabolite thus lacks an obvious role in that organism.

catabolic pathway any degradative, usually exergonic, sequence of reactions. *Compare* **anabolic pathway**. *See also* **amphibolic**.

catabolism *or* **katabolism** any metabolic process involving the breakdown of complex substances into smaller products, including the breakdown of carbon compounds with the liberation of energy for use by the cell or organism. *Compare* **anabolism**. —**catabolize** *or* **catabolise** *vb.*; **catabolic** *adj.*

catabolite any product of a **catabolic pathway**.

catabolite (gene) activator protein *abbr.*: CAP; *other names* **cAMP receptor protein**, **cAMP-regulatory protein** (*abbr.*: CRP); a protein that binds to and is activated by cAMP. It then acts as a transcription-initiation factor, binding near the operator of bacterial operons that are subject to **catabolite repression** and being necessary for their efficient transcription. It belongs to the **CRP** family of transcription factors. Example from *Haemophilus influenzae*: database code CRP_HAEIN, 224 amino acids (25.15 kDa).

catabolite inhibition a general regulatory mechanism, found in *Escherichia coli*, that controls the activity of an early reaction in carbohydrate metabolism. For instance when *E. coli* is grown in synthetic medium with radioactive galactose or lactose as the carbon source, the addition of glucose rapidly inhibits utilization of the radioactive substrate. Subsequent removal of the glucose rapidly reverses the inhibition.

catabolite repression a mechanism of genetic regulation in bacteria in which the accumulation of catabolites in the cell represses the formation of enzymes that contribute to the formation of the catabolites.

catalase EC 1.11.1.6; a widely distributed hemoprotein enzyme that catalyses the formation of O_2 + 2 H_2O from two molecules of H_2O_2; heme and manganese are cofactors. It plays an important role in removing H_2O_2 formed in peroxisomes in animals and plants and in **glyoxysomes** in plants. The molecule has seven motifs. Examples: (1) homotetramer from tomato: database code CAT1_LYCES, 492 amino acids (56.44 kDa); (2) bovine enzyme: database code NRL_7CATA, 498 amino acids (56.61 kDa); 3-D structure is known; α helical and β barrel regions are present.

catalatic of, or pertaining to, **catalase**.

catalyse *or (esp. US)* **catalyze** to influence a reaction through **catalysis**.

catalysis an increase in the rate of a chemical reaction brought about by a **catalyst**. —**catalytic** *adj.*; **catalytically** *adv.*

catalysome **1** an enzyme-containing cap found on lipid droplets in the fat body of some insects. **2** a mitochondrion-like organelle specialized for lipid metabolism, found in adipose tissue.

catalyst any substance that increases the rate of a chemical reaction but is itself unchanged at the end of the reaction. Catalysts are usually present in very low concentrations relative to those of the substances whose reaction they are catalysing.

catalytic activity an index of the actual or potential activity of a catalyst. The catalytic activity of an enzyme or an enzyme-containing preparation is defined as the property measured by the increase in the rate of conversion of a specified† chemical reaction that the enzyme produces in a specified† assay system. [†This word, in one or other position, has been misprinted as 'specific' in certain published versions of this definition.] Catalytic activity is an extensive quantity (*see* **extensive property**) and is a property of the enzyme, not of the reaction mixture; it is thus conceptually different from rate of conversion although measured by and equidimensional with it. The unit for catalytic activity is the **katal**; it may also be expressed in mol s^{-1}. Dimensions: N T^{-1}. Former terms such as catalytic ability, catalytic amount, and enzymic activity are no longer recommended. Derived quantities are **molar catalytic activity**, **specific catalytic activity**, and **catalytic activity concentration**.

catalytic activity concentration *or* **catalytic concentration** the **catalytic activity** of an enzyme per unit volume, where volume refers to that of the original enzyme-containing preparation, not that of the assay system. It may be expressed in katals per litre.

catalytic amount the amount of a substance used in a chemical reaction as a catalyst, primer, or sparker. It is generally much smaller than the stoichiometric amounts of either reactants or products. For an enzyme the term is now obsolete and replaced by **catalytic activity**.

catalytic assay a technique for measuring low concentrations (≈1 μM) of substrates in certain enzyme-catalysed reactions (e.g. $NAD(P)^+$ or coenzyme A), where simple kinetic methods are not feasible because too-rapid consumption makes reaction rates impossible to measure reliably. Conditions are arranged so that the concentration of the substrate in question is kept constant by a regeneration reaction, the substance being made to behave as an intermediate catalyst. The regeneration reaction may act also as the indicator reaction. For example, NAD^+ may be determined by coupling the reaction catalysed by alcohol dehydrogenase (EC 1.1.1.1) to the combined regeneration/indicator reaction catalysed by cytochrome *c* reductase (EC 1.6.99.3), according to the equations:

$$NAD^+ + C_2H_5OH \rightarrow NADH + CH_3CHO + H^+$$

and

$$NADH + H^+ + 2\ \text{Cyt}\ c^{3+} \rightarrow NAD^+ + 2\ \text{Cyt}\ c^{2+} + 2\ H^+.$$

The rate of increase in absorbance of Cyt c^{2+} at 550 nm is measured. If the coupled regeneration reaction does not act as an indicator reaction, the technique is known as **enzymic cycling**. *Compare* **coupled assay**.

catalytic concentration *an alternative term for* **catalytic activity concentration**.

catalytic constant *symbol*: k_{cat} *or* k_0; a measure of the catalytic potential of an enzyme, customary unit s^{-1}. In general it is the value of the velocity of the reaction, v, divided by the stoichiometric concentration of active sites, $[E]_0$, obtained by extrapolating all substrate concentrations to infinity; alternatively it can be expressed as $V_{max}/[E]_0$, where V_{max} is the **limiting rate**. k_{cat} is also known as the **turnover number**, because it represents the number of reactions catalysed per unit time by each active site.

catalytic domain *see* **domain** (def. 3).

catalytic exchange method a method for randomly labelling a compound with tritium. A solution of the compound in a tritiated hydroxylic solvent is allowed to stand in the presence of metal catalysts and either acid or base.

catalytic facilitation a process whereby the product formed by one enzyme in a complex is passed directly to the catalytic site of the next enzyme in a reaction sequence more efficiently than when the second substrate is supplied from the environment.

catalytic factor a term sometimes used of a specified enzyme to define the quantitative ratio between the rates of a chemical reaction in the presence and the absence of the enzyme but otherwise under the same conditions.

catalytic intermediate a chemical species produced during the course of a catalytic reaction, intermediate between reactants and products.

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catalytic power a measure of the ability of an enzyme to accelerate a chemical reaction.

catalytic residue any of the amino-acid residues in an enzyme that are directly involved in making or breaking covalent bonds while the enzyme is acting on a substrate.

catalytic site the site on a catalyst that is concerned with catalysis, especially as part of the **active site** of an enzyme.

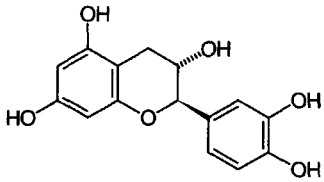
catalyze *the US spelling of* **catalyse**.

CAT assay assay of **chloramphenicol *O*-acetyltransferase**, frequently employed to detect expression of its gene in cDNA technology.

catastrophe theory *see* **error catastrophe hypothesis**.

CAT box *see* **CAAT box**.

catechin the type compound for one of the 12 classes of flavanoids. It is characterized by oxidation state (OH at C-3) of the central pyran ring. Some 70 catechins are known; e.g. (+)-catechin is (2*R*,2*S*)-3,3′,4′,5,7-flavanpentol. Catechins are among the polyphenols widely distributed in vegetable foods, arising biosynthetically from the **shikimate** pathway. (+)-Catechin produces artificial cross-links in collagen *in vitro* and has anti-tumour activity. Catechin and **curcumin** have been found to be non-toxic, non-mutagenic, non-teratogenic and excellent anti-mutagens and anti-carcinogens which are being clinically tested by the National Cancer Institute.



(+)-catechin

catechol **1** *former name for* **pyrocatechol**. **2** any aromatic *o*-diol; any compound containing a pyrocatechol nucleus or substituent. *Compare* **hydroquinone** (def. 2), **quinone** (def. 2).

catecholamine any of a group of physiologically important **biogenic amines** that possess a **catechol** (def. 2) (i.e. 3,4-dihydroxyphenyl) nucleus and are derivatives of 3,4-dihydroxyphenylethylamine. They include **adrenaline**, (epinephrine) **noradrenaline** (norepinephrine), and **dopamine**. Catecholamines have various physiological roles, particularly as neurotransmitters, and produce effects in the brain, the cardiovascular system, and other organs; they also help to regulate carbohydrate and fat metabolism.

catechol melanin any of various deep-brown or black plant pigments, so called because they yield catechol on alkali fusion. *See also* **melanin**.

catechol-*O*-methyltransferase EC 2.1.1.6; *systematic name*: *S*-adenosyl-L-methionine:catechol *O*-methyltransferase. An enzyme found primarily in non-neuronal tissues and catecholamine-releasing neurons, especially in the periphery; it effects *O*-methylation of catecholamines and their deaminated metabolites, but is less active against catechols. It catalyses the reaction between *S*-adenosyl-L-methionine and catechol to form *S*-adenosyl-L-homocysteine and guaiacol; in catecholamines it methylates the phenolic group at position 4. This inactivates catecholamine neurotransmitters and catechol hormones. Example from human: database code COMT_HUMAN, 271 amino acids (30.00 kDa), is the membrane-bound form; a cytosolic form (residues 52–271) lacks the transmembrane signal anchor.

catechol oxidase *see* **polyphenol oxidase**. *See also* **monophenol monooxygenase**.

catenane any type of compound containing two or more rings that are interlocked but not covalently joined; i.e. resembling the links of a chain. An example is an interlocked circular duplex DNA molecule found in mitochondria. *Compare* **concatemer**.

catenate **1** to interlock, without covalent bonding, two or more circular structures, e.g. cyclic molecules. **2** linked as the interlocked rings of a chain. *Compare* **concatenate**. —**catenated** *adj.*; **catenation** *n.*

cathepsin any of a group of intracellular peptide hydrolases.

cathepsin B EC 3.4.22.1; *other name*: lysosomal cysteine endopeptidase. An enzyme that catalyses the hydrolysis of proteins with broad specificity for peptide bonds; preferentially it cleaves -Arg-Arg-|-Xaa- bonds in small substrates. It is a glycoprotein dimer comprising a heavy chain and a light chain cross-linked by a disulfide bond. Example (human) precursor: database code CATB_HUMAN, 339 amino acids (37.76 kDa).

cathepsin C EC 3.4.14.1; *recommended name*: dipeptidyl peptidase I. An enzyme that catalyses the hydrolysis of dipeptides from the N terminus of a polypeptide, except where the N-terminal residue is Arg or Lys, or where the adjacent amino acid is Pro. It also catalyses the transfer of dipeptide residues.

cathepsin D EC 3.4.23.5; a lysosomal aspartic endopeptidase that is active in intracellular protein breakdown. It has a specificity similar to, but narrower than, that of **pepsin A**. The molecule comprises a light chain and a heavy chain. Example (human) precursor: database code CATD_HUMAN, 412 amino acids (44.50 kDa).

cathepsin E EC 3.4.23.34; an aspartic endopeptidase with similar activity to **cathepsin D**, but found in lymphoid-associated tissue. It may have a role in immune function. Example (human) precursor: database code CATE_HUMAN, 396 amino acids (42.74 kDa).

cathepsin G EC 3.4.21.20; a glycoprotein serine endopeptidase with a specificity similar to that of **chymotrypsin**. It is found in the lysosomes of polymorphonuclear leukocytes. Example (human) precursor: database code CATG_HUMAN, 255 amino acids (28.80 kDa).

cathepsin H EC 3.4.22.16; a lysosomal cysteine endopeptidase that also acts as an aminopeptidase on peptide substrates with a free N terminus. It is composed of a minichain and a large chain; the large chain may be split into heavy and light chains; all chains are held together by disulfide bonds. Example (human) precursor: database code CATH_HUMAN, 335 amino acids (37.36 kDa).

cathepsin L EC 3.4.22.15; *other name*: major excreted protease (*abbr.*: MEP). A lysosomal cysteine endopeptidase that hydrolyses proteins but not acylamino acid esters, and has no peptidyl-dipeptidase activity – the activity is similar to that of **papain**. It is found in rat-liver and other mammalian lysosomes, and is inhibited by **leupeptin**. The molecule is a dimer of a heavy and a light chain linked by disulfide bonds. Example (human) precursor: database code CATL_HUMAN, 333 amino acids (37.52 kDa).

cathepsin S EC 3.4.22.27; a lysosomal single-subunit cysteine endopeptidase with similar activity to **cathepsin L** but more activity for -Val-Val-Arg-|-Xaa. Example (human) precursor: database code CATS_HUMAN, 331 amino acids (37.44 kDa).

cathode *or (formerly)* **kathode** **1** the electrode of an electrolysis cell or electrophoresis apparatus towards which cations of the electrolyte migrate under the influence of an electric field applied between the electrodes. **2** negative electrode: the electrode, pole, or terminal of a discharge tube, solid-state rectifier, thermionic valve, or other apparatus by which conventional electric current returns to an external source; i.e. the electrode through which electrons flow into such a device. **3** the positive pole or terminal of an electric (primary or secondary) cell or battery (of cells); i.e. the pole from which electrons emerge from such a device. *Compare* **anode**. —**cathodal, cathodic,** *or* **cathodical** *adj.*; **cathodally** *or* **cathodically** *adv.*

cathode-ray tube a vacuum tube in which a beam of electrons is emitted and focused by an electron gun onto a fluorescent screen. The beam can be deflected by horizontal and vertical electrostatic or magnetic fields to produce a visual display of

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electric signals, as in a television tube or cathode-ray oscilloscope.

catholyte in isoelectric focusing, the electrolyte that is in immediate contact with the cathode.

cation *or (formerly)* **kation** any **ion** with a net positive charge. In a solution being electrolysed, a cation migrates towards the **cathode**. *Compare* **anion**. —**cationic** *adj*.

cation exchange the process of **ion exchange** in which one cation is exchanged for another cation.

cation exchanger any **ion exchanger** that is able to exchange cations with the surrounding solution. *See also* **ion-exchange resin**.

cationic acid any acid that carries a positive charge, i.e. is a **cation**.

cationic detergent any **detergent** in which the polar part of the molecule carries one or more positive charges.

cationized ferritin a polycationic derivative of **ferritin** prepared by coupling horse-spleen ferritin with *N*,*N*-dimethyl-1,3-propanediamine, most of the carboxyl groups on the ferritin molecule thereby being converted into positively charged tertiary amino groups. It is useful for labelling negatively charged groups on cell surfaces, where the ferritin particles may easily be identified by electron microscopy because of their electron-dense iron cores.

cationmotive describing any enzyme, enzyme system, or other process that produces the vectorial movement of cations, especially across a biomembrane. The particular cation(s) may be specified, e.g. protonmotive, Na^+/K^+-motive.

CAU a codon in mRNA for L-histidine.

caudal a homeodomain transcription factor which forms a concentration gradient in the opposite direction to that of **bicoid protein**, possibly as a result of the translation control exerted on the caudal mRNA by bicoid.

cauliflower mosaic virus a double-stranded DNA virus that is a potential recombinant vector for plants.

caulimovirus any double-stranded DNA plant virus belonging to the *Caulimovirus* group, the type member of which is the **cauliflower mosaic virus**.

caustic soda *see* **soda**.

caveola (*pl.* **caveolae**) a closed plasmalemmal vesicle that is thought to remain attached to the plasma membrane while extruding into the cytoplasm materials taken up from the outside of the cell. It is rich in glycosylphosphatidylinositol (GPI)-anchored proteins. [From Latin *cavea*, a small cavity.]

caveolin a protein that lines the cytoplasmic surface of a **caveola**. Example from dog: database code CAVE_CANFA, 178 amino acids (20.6 kDa).

CBF *abbr. for* centromere binding factor (*see* **centromere binding proteins**).

CBG *abbr. for* cortisol binding globulin. *See* **transcortin**.

CBL a protooncogene related to v-*cbl*, the nuclear oncogene of Cas NS-1 retrovirus, named from Casitas B-lineage lymphoma. The function of the normal protein is unknown, but it may be a transcriptional regulator. v-*cbl* encodes a truncated form of Cbl, which has lost a C-terminal leucine zipper and a 208-residue proline-rich region. Example, human protooncogene product c-Cbl: database code CBL_HUMAN, 906 amino acids (99.65 kDa).

Cbm *symbol for* carbamoyl.

CBN *abbr. for* (IUPAC-IUB) Commission on Biochemical Nomenclature; now succeeded by **JCBN**.

Cbz *symbol for* the benzyloxycarbonyl group.

cc *symbol for* cubic centimetre (cm^3 is preferred).

CC *abbr. for* cholecalciferol (**vitamin D_3** is preferred).

CCA a codon in mRNA for L-proline.

C_{55} carrier lipid *or* **C_{55} lipid carrier** *an alternative name for* **undecaprenol**.

CCC **1** a codon in mRNA for L-proline. **2** *abbr. for* β-chloroethyltrimethylammonium chloride; an inhibitor of gibberellin synthesis in plants.

cccDNA *see* **DNA**.

CCCP *abbr. for* carbonyl cyanide *m*-chlorophenylhydrazone, a powerful uncoupler of oxidative phosphorylation.

C cell the distinctive type of apud cell that secretes the polypeptide hormone **calcitonin**. In mammals C cells are found predominantly in the thyroid gland (when they are also known as **parafollicular cells**), and in some mammals and birds they also occur in the parathyroid gland and the thymus. In other vertebrates the cell type is present mainly in the discrete **ultimobranchial body** and the lung. [The name C cell was chosen to signify calcitonin-secreting cell.]

CCG a codon in mRNA for L-proline.

CCK *abbr. for* cholecystokinin.

CCK cell *see* **I cell**.

CCK-PZ *abbr. for* cholecystokinin–pancreozymin. *See* **cholecystokinin**.

cCMP *abbr. for* cyclic CMP.

C_1 compound *or* **one-carbon compound** *or* **single-carbon compound** any (real or hypothetical) organic compound that consists of a single carbon atom with attached hydrogen atom(s), and sometimes also an oxygen atom or imino group, and that functions as a unit in metabolism. Examples include the methyl group of *S*-adenosylmethionine or the iminomethyl-formimidoyl- (or formimino-), formyl-, hydroxymethyl-, methyl-, methylene-, and methenyl- groups of tetrahydrofolate coenzymes.

C3/C5 convertase *see* **complement**.

C5 convertase *see* **complement**.

CCP *abbr. for* Collaborative Computational Programs; an initiative, started in the UK, for the development and distribution of software for scientific applications. Programs include: CCP4 (crystallographic software), CCP5 (molecular dynamics), and CCP11 (sequence analysis).

CCU a codon in mRNA for L-proline.

C_3 cycle *an alternative name for* **reductive pentose phosphate cycle**.

C_4 cycle *an alternative name for* the **Hatch–Slack pathway**.

cd *symbol for* candela.

Cd *symbol for* cadmium.

CD *abbr. for* **1** circular dichroism. **2** cluster of differentiation *or* cluster determinant; *see* **CD marker**. **3** compact disc.

c-di-GMP *abbr. for* cyclic diguanylic acid.

CD4 a **CD marker** that occurs on T-helper cells and is involved in MHC class II restricted interactions. It is down-regulated by HIV infection. Example, T-cell CD4 antigen (precursor) from human: database code CD4_HUMAN, 458 amino acids (51.05 kDa); 3-D structure known; a type I membrane glycoprotein of the immunoglobulin superfamily.

CD8 a **CD marker** that occurs on human cytotoxic T-cells and suppressor T-cells. It is associated with MHC class I restricted interactions. It is a heterodimer of an α and β chain and isoforms of the β chain result from alternative splicing. The α chain binds to the MHC α_3 domain. Examples, α chain (precursor): database code CD8A_HUMAN, 235 amino acids (25.73 kDa); β_1 chain (precursor): database code C8B1_HUMAN 210 amino acids (23.72 kDa).

CD44 *other names*: phagocyte glycoprotein I; lymph node homing receptor; HERMES antigen; extracellular matrix receptor III. A cell **adhesion molecule** that is constitutively expressed on the surface of B and T cells, monocytes, neutrophils, epithelial cells, fibroblasts, glial cells, and myocytes. It has a molecular mass of 85–90 kDa and plays a general role in cell adhesion, including lymphocyte homing; it binds to collagen and hyaluronate. Example from horse: database code CD44_HORSE, 359 amino acids (38.99 kDa).

CD59 a glycoprotein that is a potent inhibitor of complement membrane attack complex (MAC); it acts after C5b8 assembly (*see* **complement**). It is also involved in signal transduction for T-cell activation, being complexed to a protein tyrosine kinase. It is attached to the membrane by a **GPI-anchor**. Example (human) precursor: database code CD59_HUMAN, 128 amino acids (14.16 kDa).

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CD66 *see* **carcinoembryonic antigen**.
CD66d *see* **carcinoembryonic antigen**.
CD66e *see* **carcinoembryonic antigen**.
CD79 *see* **B cell antigen receptor complex associated protein**.
***cdc* gene** *abbr. for* cell-division-cycle gene. Many genes are now known that encode proteins essential for cell division. These were initially identified in yeast, using temperature-sensitive mutants that divide at low temperature but which at high temperature arrest at a point in the cell-division cycle at which expression of the mutated gene would normally be required. The yeast genes were named in a series *cdc1*, *cdc2*, etc. Homologues of these genes have since been found in many other species, but the *cdc* nomenclature is used specifically for the fission yeast, *Schizosaccharomyces pombe*. The convention Cdc followed by a numeral is used for the protein products of these genes. Many products identified by this method were found not to be directly involved in the control of cell division, being proteins such as DNA polymerases. Some of those that are involved in cell-division control are (all database examples are from yeast):

Cdc2, a major cell regulatory protein, with counterparts in all eukaryotic cells. *cdc2* is homologous to *CDC28* in budding yeast. Cdc2 is a Ser/Thr protein kinase, alternatively denoted $p34^{cdc2}$, and regulated by cyclin B. $p34^{cdc2}$ and cyclin B comprise **maturation promoting factor** (MPF). Cdc2 is the patriarch of a family of cyclin-dependent kinases; Cdc2 is Cdk1. Example from *S. pombe*: database code CC2_SCHPO, 297 amino acids (34.36 kDa).

cdc25 encodes a protein phosphatase that positively regulates $p34^{cdc2}$ by dephosphorylation of Tyr^{15}. Entry to mitosis is negatively regulated by ***wee 1***, a gene in *S. pombe* that encodes a protein tyrosine kinase. Its action on mitosis results from phosphorylation of Tyr^{15} of $p34^{cdc2}$. Note: *CDC25* from budding yeast encodes a guanine nucleotide exchange protein.

Cdc28, a Ser/Thr protein kinase required for completion of both the START transition of the cycle and also the G_2/M transition: database code CC28_YEAST, 298 amino acids (34.02 kDa);

Cdc31, an **EF-hand** protein involved in microtubular organization: database code CC31_YEAST, 298 amino acids (18.73 kDa);

Cdc46, a protein mobilized from the cytoplasm to the nucleus after mitosis, and a potential ATP-binding protein: database code CC46_YEAST, 775 amino acids (86.31 kDa);

Cdc48, a putative ATP-binding protein involved in spindle formation: database code CC48_YEAST, 834 amino acids (91.77 kDa).

CDE *abbr. for* centromere DNA element; CDE-I is a group of DNA sequences, RTCACRTG, found in centromeres and some promoters. *See also* **centromere-binding proteins**.
CD59 glycoprotein precursor *see* **membrane attack complex inhibition factor**.
CDH *abbr. for* ceramide dihexoside ($Cer(Hex)_2$ is preferred).
CDI *abbr. for* *N*,*N*′-carbonyldiimidazole; 1,1′-carbonylbis-1*H*-imidazole, a reagent used in the synthesis of nucleotide triphosphates and peptides, and for cross-linking proteins.
Cdk *abbr. for* cell division protein kinase.
CD marker *(in immunology)* any of a series of antigenically distinct molecules occurring on the surface of leukocytes and other cell types, and used in the characterization of such cells. More than 80 individual CD marker molecules are recognized, as identified by **monoclonal antibodies**. The most frequently encountered CD molecules are those used to distinguish T cells. CD2 is present on all T cells and is involved in antigen-non-specific activation. CD3 is also present on all T cells and is an invariant part of the T-cell antigen receptor involved in antigen-specific T-cell activation. **CD4** occurs on T-helper cells and is involved in MHC class II restricted interactions, **CD8** occurs on cytotoxic T cells and is involved in MHC class I restricted interactions. *See also* **CD44**, **CD59**. Other CD markers listed here under other names include CD16 (*see* **Fc receptor**), CD29 (*see* **VLA**), CD31 (*see* **PECAM**), CD32 (*see* **Fc receptor**), CD49a and CD51 (*see* **VLA**), CD50 and CD54 (*see* **ICAM**), CD62 (*see* **selectin**), CD64 (*see* **Fc receptor**), CD102 (*see* **ICAM**), and CD106 (*see* **VCAM**). [From 'cluster of differentiation'.]
cDNA *abbr. for* complementary DNA.
C-DNA *abbr. for* C form of DNA.
cDNA clone any bacterial cell transformed by a plasmid containing a **complementary DNA** copy of an RNA molecule.
cDNA library a collection of cloned recombinant cDNA, usually in bacteria or yeast. The clones represent cDNAs prepared from all the mRNAs in any particular species or organ.
CDP *abbr. for* **1** cytidine 5′-diphosphate *or* the group cytidine(5′)diphospho. **2** cardiodilatin related peptide; *see* **natriuretic peptide**.
CDPcholine *see* **cytidine(5′)diphosphocholine**.
CDPdiacylglycerol *see* **cytidine(5′)diphosphodiacylglycerol**.
CDPdiacylglycerol–inositol 3-phosphatidyltransferase EC 2.7.8.11; *other names*: phosphatidylinositol synthase; CDPdiacylglyceride–inositol phosphatidyltransferase; an enzyme that catalyses the formation of phosphatidyl-1-D-*myo*-inositol from CDPdiacylglycerol and *myo*-inositol with release of CMP. It is a component of the pathway for the biosynthesis of phosphatidylinositol and also for its resynthesis after activation of the **phosphatidylinositol cycle**. Example from yeast: database code PIS_YEAST, 220 amino acids (24.80 kDa).
CDPdiacylglycerol–serine *O*-phosphatidyltransferase EC 2.7.8.8; *systematic name*: CDPdiacylglycerol:L-serine 3-*O*-phosphatidyltransferase; *other names*: phosphatidylserine synthase; CDPdiglyceride–serine *O*-phosphatidyltransferase. It is an enzyme of the pathway that effects *de novo* synthesis of phosphatidylserine. It catalyses the formation of *O*-*sn*-phosphatidyl-L-serine from CDPdiacylglycerol and L-serine with the release of CMP. Example from *Escherichia coli*: database code PSS_ECOLI, 452 amino acids (52.76 kDa). Example from *Saccharomyces cerevisiae*: database code PSS_YEAST, 275 amino acids (30.67 kDa).
CDPethanolamine *see* **cytidine(5′)diphosphoethanolamine**.
CDP-glycerol pyrophosphorylase *see* **glycerol-3-phosphate cytidylyltransferase**.
CDPK *abbr. for* calmodulin-like domain protein kinase.
CDR *abbr. for* calcium-dependent regulator protein (i.e. **calmodulin**).
CDTA *abbr. for* *trans*-cyclohexylene-1,2-diamine-*N*,*N*,*N*′,*N*′-tetraacetate, the anion of *trans*-1,2-diaminocyclohexane-*N*,*N*,*N*′,*N*′-tetraacetic acid. A **chelating agent** with a high affinity for Mg^{2+}; the abbreviation is also used for its partially or fully protonated forms.
Ce *symbol for* cerium.
C_xE_y a series of non-ionic detergents useful for the solubilization of membrane-bound proteins in their native state. They include $C_{10}E_6$, hexaethyleneglycol mono-*n*-decyl ether; $C_{10}E_8$, octaethyleneglycol mono-*n*-decyl ether; $C_{12}E_6$, hexaethyleneglycol mono-*n*-dodecyl ether; $C_{12}E_8$ octaethyleneglycol mono-*n*-dodecyl ether; and $C_{12}E_9$, nonaethyleneglycol mono-*n*-dodecyl ether; the latter two are constituents of the proprietary detergent Lubrol-PX a detergent useful for the solubilization of membrane-bound proteins in their native state.
CEA *abbr. for* carcinoembryonic antigen.
CEA gene member 1 *see* **carcinoembryonic antigen**.
Cech, Thomas Robert (1947–) US chemist, biochemist, and molecular biologist; Nobel Laureate in Chemistry (1989) jointly with S. Altman 'for their discovery of catalytic properties of RNA'.
cecropin any of a group of small, basic polypeptides with potent antibacterial activity. Cecropins are active against *Escherichia coli* and several other Gram-negative species, and are isolated from the cecropia moth, *Hyalophora cecropia*, and several other insects.
CEF10 *or* **CEF-10** a secreted protein that is implicated in

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growth regulation. It is induced by v-*src* and belongs to a family of growth regulators that includes **connective tissue growth factor**. Example (precursor) from chicken: database code CE10_CHICK, 375 amino acids (40.60 kDa).

Cek a chick gene encoding receptor-type protein tyrosine kinases, and named from chicken embryo kinase. The protein product Cek-1 is the chicken **fibroblast growth factor** receptor; Cek-2 and Cek-3 are related to ***Bek***; Cek-4 and Cek-5 are homologous to ***Eph***.

celiac *or (esp. Brit.)* **coeliac** of, or belonging to, the abdominal cavity.

celiac disease *or (Brit.)* **coeliac disease** *or* **gluten enteropathy** *or* **nontropical sprue** a condition caused by sensitivity of the mucosa of the upper small intestine to the α-gliadin component of **gluten** in wheat and rye. Characterized by diarrhoea and malabsorption, it can be relieved by elimination of gluten from the diet.

Celite *proprietary name for* preparations of amorphous diatomaceous silica, used as a filter-aid and in partition chromatography.

cell **1** the basic structural unit of all living organisms; it typically comprises a small, usually microscopic, discrete mass of organelle-containing cytoplasm, bounded externally by a membrane. Each cell is capable of interacting with other cells and performing all the fundamental functions of life. In plants the cell usually also includes the cell wall. Originally the term referred to the bounding wall of a plant cell that had lost its living content. *See also* **+cyte**, **cyto+**. **2** a container for liquid during measurement or separation procedures, such as dialysis, electric conductivity measurement, electrolysis, microdiffusion, moving boundary electrophoresis, analytical ultracentrifugation, ultrafiltration, and (spectro)photometry; *see also* **cuvette**. **3** or **electric cell** a device for producing electric current by converting chemical energy into electric energy; it consists of two electrodes in contact with an electrolyte. **4** *(in crystallography) see* **unit cell**. —**cellular** *adj*.

cell-adhesion molecule *see* **adhesion molecules**.

cell body *an alternative term for* **perikaryon**.

cell-bound antibody *or* **cell-fixed antibody** any antibody molecule that is bound to the surface of a cell, e.g. an **incomplete antibody** (def. 1) or a **cytophilic antibody**.

cell coat *another name for* the **glycocalyx**.

cell cortex the part of the microtrabecular lattice lying just under the outer cell membrane of certain protozoans, e.g. paramecia.

cell counter any device for determining the number of cells in a known volume of a liquid suspension. *See* **Coulter counter**, **flow cytometer**, **hemocytometer**.

cell culture *see* **tissue culture**.

cell cycle the period between the formation of a cell by division of its mother cell and the time when the cell itself divides to form two daughter cells. *See also* **cell-division cycle**, **DNA cycle**.

cell-cycle engine all the biochemical components, and the reactions between them, that cause the periodic activation and inactivation of **M-phase-promoting factor** during cell maturation.

cell differentiation *see* **differentiation**.

cell-division cycle the pattern of DNA synthesis in dividing eukaryotic cells. It is divided into four periods: G_1 is the first 'gap' in DNA synthesis between **telophase** and the period of DNA synthesis, designated S. This S phase is followed by G_2, the second gap in DNA synthesis. This runs on into the period of **mitosis**, M, which lasts from early **prophase** to late **telophase**.

cell division protein kinase *abbr.*: CDK; any of various protein kinase enzymes involved in the regulation of **cyclin** activity, such as CDC20. *See also* ***cdc***.

cell-fixed antibody *an alternative name for* **cell-bound antibody**.

cell fractionation the fractionation of disrupted cells into their subcellular components.

cell-free extract a fluid, made by breaking open cells, that contains most of the constituents of the cells in question but no intact cells.

cell-free system any experimental system composed of subcellular fractions and/or cell-free extracts. Cell-free systems for amino-acid incorporation (protein synthesis) generally contain ribosomes, natural or synthetic mRNA, tRNAs, enzymes, amino acids, an ATP generating system, GTP, buffer, certain inorganic salts, and some organic compounds.

cell fusion the formation of a single hybrid cell containing the nuclei and cytoplasms from different cells. It may be induced by treatment of a mixed cell population with certain **fusogens** (e.g. killed Sendai virus or polyethylene glycol). It is an important step in the technique of forming **hybridoma cells** for the production of **monoclonal antibodies**.

cell junction a specialized region of connection between two cells or between a cell and the extracellular matrix. *See also* **desmosome**, **gap junction**, **hemidesmosome**, **tight junction**.

cell line a population of cells cultured *in vitro* that are descended through one or more generations (and possibly subcultures) from a single primary culture. The cells of such a population share common characteristics.

cell locomotion *see* **cell migration**.

cell matrix *see* **extracellular matrix**.

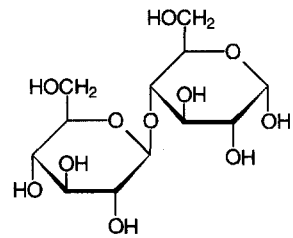
cell-mediated immunity specific immunity that depends on the presence of T lymphocytes. It is responsible for, e.g., allograft rejection, delayed hypersensitivity, and tuberculin test reactions, and is important in the organism's defence against viral and some bacterial infections.

cell membrane any **membrane** found in a cell. The term is sometimes used loosely to indicate the **plasma membrane**. *See also* **cytoplasmic membrane**.

cell migration the active movement of a cell from one location to another, particularly the migration of a cell over a surface.

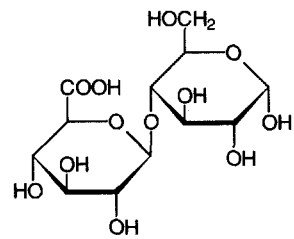
β-cellobiase *another name for* β-glucosidase; *see* **glucosidase**.

cellobiose 4-*O*-β-D-glucopyranosyl-D-glucose; a disaccharide that represents the basic repeating unit of **cellulose**; it is liberated by **cellulase**.



α-anomer

cellobiuronic acid 4-*O*-β-D-glucopyranuronosyl-D-glucose; *condensed form*: GlcA(β1-4)Glc. It is a component of, e.g., type III pneumococcal bacterial capsule polysaccharides.



α-anomer

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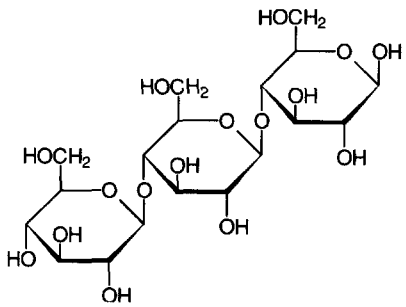
cellophane a form of transparent, flexible sheeting made from regenerated **cellulose**; originally a proprietary name.

Cellosolve *proprietary name for* a range of ethanediol monoalkyl ethers, especially 2-ethoxyethanol. They are useful as solvents, e.g. in liquid scintillation mixtures, to facilitate the dispersion of aqueous samples in organic solvents.

cellotetraose a tetrasaccharide composed of D-glucose units in β1–4 linkage.

cellotriose the trisaccharide *O*-β-D-glucopyranosyl-(1–4)-*O*-β-D-glucopyranosyl-(1-4)-D-glucose; *condensed form*: Glc(β1-4)Glc(β1-4)Glc.



β-D-pyranose form

cell plate the nascent cell membrane and cell wall structure that forms between the two daughter nuclei near the centre of a dividing plant cell. It develops at the equatorial region of the **phragmoplast**. It grows outwards to join with the lateral walls and form two daughter cells.

cell sorter any **flow sorter** for sorting cells in liquid suspension, on the basis of some characteristic that is detectable by the sorter.

cell-surface protein *abbr.*: CSP; *an alternative name for* **fibronectin**.

cellubrevin a **synaptobrevin** homologue that is involved in membrane traffic as part of a constitutively recycling pathway. With VAMP proteins it is a component of the machinery controlling docking and fusion of secretory vesicles with their target membrane. It is a ubiquitous substrate for **tetanus toxin** light chain. Example from *Rattus norvegicus*: database code S35077, 103 amino acids (11.47 kDa).

cellular affinity the tendency of cells to adhere specifically to cells of the same type, but not to cells of a different type. This property is lost in cancer cells.

cellular immunity **1** the increased ability of phagocytic cells to destroy parasitic organisms, i.e. macrophage immunity. **2** *an alternative name for* **cell-mediated immunity**.

cellulase **1** EC 3.2.1.4; *other names*: endoglucanase; endo-1,4-β-glucanase; carboxymethyl cellulase. An enzyme that catalyses the endohydrolysis of 1,4-β-D-glucosidic linkages in **cellulose**, thereby hydrolysing cellulose to cellobiose. It causes abscission in plants, and its synthesis is stimulated by ethylene. Microbial cellulases play an important part in the digestion of cellulose by ruminants. **2** any lytic enzyme whose substrate is cellulose. *See* **cellulose 1,4-β-cellobiosidase**, **glucosidase**. Example from *Cellulomonas uda*: database code GUN_CELUD, 359 amino acids (40.64 kDa).

cellule **1** (*archaic*) a minute cavity or very small **cell**. **2** *a former name for* a **liposome** bounded by a single lipid bilayer.

cellulose a linear β1–4 **glucan** of molecular mass 50–400 kDa with the pyranose units in the $^4C_1$ conformation. It is predominantly a plant polysaccharide though it also occurs in some tunicates. Cellulose microfibrils are major components of plant cell walls. Cellulose is insoluble in water but will dissolve in ammoniacal solutions of cupric salts. It is often said to be the most abundant organic compound in the biosphere, but this distinction has also been accorded to the **hopanoids**.

cellulose 1,4-β-cellobiosidase EC 3.2.1.91; *other names*: exoglucanase; exocellobiohydrolase; 1,4-β-cellobiohydrolase. An enzyme that catalyses the hydrolysis of 1,4-β-D-glucosidic linkages in cellulose and cellotetraose, releasing cellobiose from the nonreducing ends of the chains. Example (precursor) from *Trichoderma reesei*: database code GUX1_TRIRE, 513 amino acids (54.01 kDa); 3-D structure of C-terminal domain: database code NRL_1CBH, 36 amino-acid fragment (3.74 kDa).

cellulosic **1** of, or pertaining to, cellulose; of the nature of cellulose; composed (primarily) of cellulose; derived from or made by chemical modification of cellulose. **2** a substance made from cellulose or a derivative of cellulose.

cellulolysis the process of hydrolysing cellulose. —**cellulolytic** *adj.*

cell wall the rigid or semi-rigid envelope lying outside the **cell membrane** of plant, fungal, and most prokaryotic cells maintaining their shape and protecting them from osmotic lysis. In prokaryotes it lies inside any capsule and slime layer, usually consists mainly of **peptidoglycan**, and can be removed by various techniques with retention of its three-dimensional form. In fungi the cell wall is composed largely of polysaccharides, while in plants it is made up of cellulose and, often, lignin.

Celsius temperature *symbol*: θ *or* t; a temperature defined as the excess of the thermodynamic temperature, T, over 273.15 K; i.e. $\theta = T - 273.15$, where θ is measured in °C (i.e. **degrees Celsius**, formerly called degrees centigrade) and T is measured in **kelvins**. It is identical with centigrade temperature. [After Anders Celsius (1701–44), Swedish astronomer.]

centi- *symbol*: c; SI prefix denoting 10^{-2}.

centigrade temperature *former name for* **Celsius temperature**.

centimetre–gram–second system *see* **cgs system**.

centimorgan *or* **centiMorgan** *abbr.*: cM; a unit of **map distance** used in genetic mapping, equal to 1% crossover found in recombination studies; 1 cM equals 1 map unit. Hence, if two genes are separated by 1 cM, there is a 1% probability of recombination in a single meiotic event.

central dogma a fundamental principle of molecular biology, first articulated by Francis **Crick** in 1958. He wrote that the central dogma states that once 'information' has passed into protein *it cannot get out again*. In more detail, the transfer of information from nucleic acid to nucleic acid, or from nucleic acid to protein may be possible, but transfer from protein to protein, or from protein to nucleic acid is impossible. Information means here the *precise* determination of sequence, either of bases in the nucleic acid or of amino-acid residues in the protein. The dogma has been taken to relate primarily to the following transfers of information that can occur in all cells: DNA → DNA, DNA → RNA, and RNA → protein. However, the transfer of information from RNA to RNA occurs in the replication of RNA viruses. The transfer of information from RNA to DNA occurs following infection of a cell with a retrovirus; the DNA is then incorporated into the host genome. When challenged that the reverse transfer of information from RNA to DNA by retroviruses contradicted the dogma, Crick refuted the challenge by drawing attention to the fact that as originally formulated the dogma permitted the transfer of information from (any) nucleic acid to (any other) nucleic acid (although the action of retroviruses was not known at that time) and that the essential point was that *sequence* information could not be passed from protein to nucleic acid, or from protein to protein.

central nervous system *abbr.*: CNS; the part of the nervous system of an animal that contains a high concentration of cell bodies and synapses and is the main site of integration of nervous activity. In higher animals it is isolated from the circulation by the **blood–brain barrier**. It consists essentially of a brain or cerebral ganglia, and a nerve cord, which may be dorsal or ventral, single or double. *Compare* **peripheral nervous system**.

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centrifugal 1 moving, acting, or tending to act away from a centre or axis. 2 of, pertaining to, or operated by a **centrifugal force**. 3 *(in botany)* developing outwards from a centre, as the flowers of certain types of inflorescence. 4 *(in physiology)* sending nerve impulses from a central location to parts supplied by that nerve; **efferent**. *Compare* **centripetal**.

centrifugal analyser *or* **centrifugal fast analyser** an apparatus widely used in clinical chemical laboratories for the simultaneous and very rapid chemical, biochemical, or immunochemical determination of one particular constituent in each of a large number of samples. Basically it consists of an appropriately designed transfer disk into which reagent(s) and samples are discretely and automatically pipetted. When loaded, the transfer disk is placed in the centre of a cuvette rotor in the centrifuge, and the rotor is accelerated. Reagent(s) and each sample are mixed together as they are radially propelled along specially shaped channels into the cuvettes. Absorbance, fluorescence, or other measurements are then made automatically on the cuvettes as they are rotating. The whole process, including data handling, is controlled by a computer.

centrifugal elutriation a technique in which cells or other particles are separated by **elutriation** in a specially constructed centrifuge rotor; the increased gravitational field resulting from centrifugation speeds up separation of the particles.

centrifugal field any space in which a **centrifugal force** is operating, as in the spinning rotor of a centrifuge.

centrifugal force a force acting radially outwards on any body moving in a curved path, equal and opposite to the **centripetal force**. The centrifugal force on a body of mass m, moving in a circular path of radius r, with velocity v, is: mv_2/r.

centrifuge 1 an apparatus in which fluids may be rotated rapidly so that substances (solutes or dispersed particles) of different densities may be separated by centrifugal force. 2 to rotate rapidly in a centrifuge. —**centrifugation** *n*.

centrin *an alternative name for* **caltractin**.

centriole a cellular organelle, found close to the nucleus in many eukaryotic cells, consisting of a small cylinder with microtubular walls, 300–500 nm long and 120–150 nm in diameter. It contains nine short, parallel, peripheral microtubular fibrils, each fibril consisting of one complete **microtubule** fused to two incomplete microtubules. Cells usually have two centrioles, lying at right angles to each other. At division, each pair of centrioles generates another pair and the twin pairs form the poles of the mitotic spindle. *Compare* **basal body**.

centripetal 1 moving, acting, or tending to act towards a centre or axis. 2 of, pertaining to, or operated by a **centripetal force**. 3 *(in botany)* developing inwards from the outside, as the flowers of certain inflorescences. 4 *(in physiology)* sending nerve impulses towards a central location from peripheral parts supplied by that nerve; **afferent**. *Compare* **centrifugal**.

centripetal force a force acting radially inwards on any body moving in a curved path; it constrains the body to a curved path. It is equal and opposite to the **centrifugal force**.

centromere the region of a eukaryotic chromosome that is attached to the spindle during nuclear division. It is defined genetically as the region of the chromosome that always segregates at the first division of meiosis; i.e. the region of the chromosome in which no **crossing over** occurs. At the start of M phase, each chromosome consists of two sister chromatids with a constriction at a point which forms the centromere. During late prophase two **kinetochores** assemble on each centromere, one kinetochore on each sister chromatid.

centromere-binding proteins proteins from, e.g., the yeast **kinetochore** that are able to bind centromere DNA; examples from yeast: centromere-binding protein 1: database code CBF1_YEAST, 351 amino acids (39.40 kDa); a protein that binds to a sequence in centromere DNA known as CDE-I; it is a helix-turn-helix protein; (2) centromere-binding protein 2: sequence of the 110 kDa subunit: database code CBF2_YEAST, 956 amino acids (111.79 kDa); a complex involving a larger (240 kDa) subunit of this protein also binds to CDE-I and is involved in spindle formation.

centrosome a structure occurring close to the nucleus during **interphase** in many eukaryotic cells. It comprises a pair of **centrioles**, satellite bodies, and a cytoplasmic zone from which the mitotic microtubule spindle is organized. The structure of the centrosome in animal cells changes continually during the **cell-division cycle**.

centrosphere a more or less well delineated part of the cytoplasm at the poles of the spindle (*see* **mitotic spindle**).

cephaeline an alkaloid derived from *Uragoga ipecacuanha*. It is a gastric irritant, inducing emesis. See also **emetine**, **ipecachuanha**.

cephalin *a former name for* 1 **phosphatidylethanolamine**. 2 **phosphatidylserine**.

cephalosporin any of a heterogeneous group of natural and semisynthetic, often β-lactam, antibiotics. Cephalosporins C, N, and P are obtained from cultures of moulds such as *Cephalosporium acremonium*. Cephalosporins are active against a range of Gram-positive and Gram-negative bacteria.

cephalosporinase *an alternative name for* **β-lactamase** II.

Cer *symbol for* a ceramide residue. *See also* **Cer(Hex)**.

ceramidase EC 3.5.1.23; *other name*: acylsphingosine deacylase; an enzyme involved in the degradation of sphingolipids. It catalyses the hydrolysis of *N*-acylsphingosine to a fatty acid and sphingosine.

ceramide *symbol*: Cer; any *N*-acylated **sphingoid**.

ceramide cholinephosphotransferase EC 2.7.8.3; an enzyme involved in the biosynthesis of sphingomyelin by the reaction of CDPcholine with *N*-acylsphingosine with the release of CMP.

ceramide glucosyltransferase EC 2.4.1.80; an enzyme that catalyses the formation of glucosylceramides. The reaction involves the formation of D-glucosyl-*N*-acylsphingosine from UDPglucose and *N*-acylsphingosine with the release of UDP.

cercidosome an atypical mitochondrion or oxidizing body, found, e.g., in trypanosomes, whose function may primarily be to regulate the NAD^+/NADH ratio of the cytosol. [From Greek *kerkis, kerkido*, weaver's shuttle, + **+some**.]

cerebellin *see* **precerebellin**.

cerebral 1 of, or relating to, the cerebrum. 2 *(loosely)* of, or relating to the brain.

cerebrodiene a lipid, resembling **sphingosine**, that is obtained from the brain of sleep-deprived cats.

cerebroglycan an integral membrane heparan sulfate proteoglycan unique to the developing nervous system and expressed specifically during neuronal differentiation. Example from neonate rat brain: database code RATCRBGLVC, 579 amino acids (63.28 kDa).

cerebronate 2-hydroxytetracosanoate; $CH_3(CH_2)_{21}CH(OH)COO^-$; it is the 2-hydroxy derivative of lignocerate. It is enriched in brain cerebrosides, the fraction containing this fatty acid being known as **phrenosin**.

cerebrose *see* **galactose**.

cerebroside any **glycosphingolipid** that contains a monosaccharide, normally glucose or galactose, in 1-*O*-β-glycosidic linkage with the primary alcohol of an *N*-acyl **sphingoid** (ceramide). In plants the monosaccharide is normally glucose; in animals it is normally galactose, though this may vary with the tissue, glucose being present in blood cerebroside. In plants, the sphingoid is usually phytosphingosine, in animals sphingosine or dihydrosphingosine (sphinganine). Cerebrosides frequently contain large amounts of longer-chain fatty acids such as behenic (22:0), lignoceric (24:0), and nervonic (24:1) acids, and 2-hydroxy fatty acids such as cerebronic (α-OH24:0) and 2-hydroxynervonic acids. Cerebroside synthesis may proceed either by acylation of psychosine or transfer of glucose or galactose to ceramide.

cerebroside-sulfatase EC 3.1.6.8; *other name*: arylsulfatase A; an enzyme involved in the catabolism of sulfatides. It catalyses the hydrolysis of a cerebroside 3-sulfate to a cerebroside

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and sulfate. Example (precursor) from human: database code ARSA_HUMAN, 507 amino acids (53.53 kDa).

cerebrospinal fluid *abbr.*:CSF; a clear fluid, containing little protein and few cells, that fills the subarachnoid space and ventricles of the brain, and the central canal of the spinal cord.

Cerenkov counter *a variant spelling of* **Cherenkov counter**.

Cerenkov radiation *a variant spelling of* **Cherenkov radiation**.

Cer(Hex) *symbol for* ceramide monohexoside. The di- and trihexosides are symbolized by $Cer(Hex)_2$ and $Cer(Hex)_3$ respectively. *See also* **Cer**.

cerinic acid *see* **cerotoyl**.

ceroid an autofluorescent, insoluble lipopigment that accumulates in the livers of rats with nutritional cirrhosis.

cerotoyl *symbol*: Crt; *the trivial name for* hexacosanoyl, CH_3–$[CH_2]_{24}CO$–, the univalent acyl group derived from hexacosanoic acid (*also called* **certoic acid** *or (formerly)* **cerinic acid**), a saturated, unbranched, acyclic, aliphatic acid, which occurs naturally in wool fat.

certoic acid *see* **cerotoyl**.

cerulein *or (Brit.)* **caerulein** a decapeptide, pGlu-Gln-Asp-Tyr(SO_3H)-Thr-Gly-Trp-Met-Asp-PheNH_2, isolated from the skin of various frogs, e.g. *Hyla caerulea*. It is often accompanied by the nonapeptide **phyllocerulein** (*or* **phyllocaerulein**). Both have the same C-terminal pentapeptide amide sequence as porcine **cholecystokinin**. Cerulein-like peptides have been isolated from the antrum and small intestine of amphibians, in which they stimulate strongly the secretion of gastric acid.

cerulenin (2*R*,3*S*)-epoxy-4-oxo-7*E*,10*E*-dodecadienamide; an antifungal antibiotic isolated from *Cephalosporium caerulens* and other sources. It inhibits fatty-acid biosynthesis by binding with 3-oxoacyl-[acyl carrier protein] synthase (*see* **fatty acid synthase complex**) and also interferes with sterol biosynthesis by inhibiting **hydroxymethylglutaryl-CoA synthase** activity.

cerulin *a variant spelling of* **cerulein**.

ceruloplasmin *or (Brit.)* **caeruloplasmin** a bright-blue copper-containing protein found in blood plasma. It has ferroxidase activity, EC 1.16.3.1, and catalyses the reaction:

$$4\ \text{iron(II)} + 4\ H^+ + O_2 = 4\ \text{iron(III)} + 2\ H_2O.$$

It binds six or seven Cu^{2+} ions per molecule. It is important in iron metabolism and is abnormally low in hepatolenticular degeneration (Wilson's disease). It is one of the acute phase proteins, its level rising late in the acute phase. Example from human: database code CERU_HUMAN, 1065 amino acids (122.2 kDa).

ceryl *the common name for* hexacosyl, CH_3–$[CH_2]_{24}$–CH_2–, a saturated, unbranched, acyclic, alkyl group.

cesium chloride *or (esp. Brit.)* **caesium chloride** a salt that forms dense solutions in water and so is used in **isopycnic centrifugation** to separate DNA molecules of different densities.

Cet *symbol for* the carboxyethyl group, $–CH_2–CH_2–COOH$.

cetaceum *an alternative term for* **spermaceti**.

Cetavlon *a proprietary name for* **cetrimide**.

cetoleic acid *see* **docosenoic acid**.

cetrimide *or* **cetrimidum** a detergent disinfectant consisting of a mixture of alkylammonium bromides, principally **cetyltrimethylammonium bromide**. *See* **quaternary ammonium compounds**.

cetyl *or* **palmityl** *the common name for* hexadecyl, CH_3–$[CH_2]_{14}$–CH_2–, a saturated, unbranched, acyclic, alkyl group (hexadecyl is preferred).

cetyltrimethylammonium bromide *abbr.*: CTAB; hexadecyltrimethylammonium bromide; *N*,*N*,*N*-trimethyl-1-hexadecanaminium bromide; a cationic detergent useful in the solubilization of membrane proteins; aggregation number 170, CMC 1 mM. It is the principal component of **cetrimide**.

Cf *symbol for* californium.

C form of DNA *abbr.*: C-DNA *or* DNA-C; the molecular conformation adopted by fibres of the lithium salt of duplex DNA at low relative humidity (below approximately 44%). It consists of a right-handed double helix containing about 9.3 nucleotide residues per turn; otherwise it is similar to the **B form**. *See also* **A form** (def. 1), **Z form**.

CFTR *abbr. for* cystic fibrosis transmembrane conductance regulator.

CG *abbr. for* chorionic gonadotropin (*see* **choriogonadotropin**).

cg clone any crown gall **clone** (def. 1); *see* **crown gall disease**.

CGM1 *see* **carcinoembryonic antigen**.

cGMP *abbr. for* cyclic GMP; *see* **guanosine 3′,5′-phosphate**.

CGRP *abbr. for* calcitonin gene-related peptide.

cgs system *or* **CGS system** *abbr. for* centimetre–gram–second system; a metric system of units based on the centimetre (length), gram (mass), and second (time). It has now been superseded by the **SI** system.

Chaikoff homogenizer a hydraulically operated tissue or cell homogenizer in which the sample is forced through an annulus by a piston. The piston diameter relative to that of the annulus is chosen to suit the size of the component that it is desired to isolate with minimal damage.

Chain, (Sir) Ernst Boris (1906–79), German-born British chemical pathologist and biochemist remembered particularly for his part in the development of penicillin (with H. W. Florey) and semisynthetic variants of penicillin as clinically useful antibacterial agents; Nobel Laureate in Physiology or Medicine (1945) jointly with A. Fleming and H. W. Florey ' for the discovery of penicillin and its curative effect in various infectious diseases'.

chain reaction a chemical reaction in which one or more reactive intermediates are continuously regenerated, often through a repetitive cycle of elementary 'propagation' steps.

chain-termination codon *an alternative name for* **termination codon**.

chain-termination method *or* **dideoxy method** *or* **Sanger method** a rapid technique for determining nucleotide sequences in DNA in which the 2′,3′-dideoxy (or arabinonucleoside) analogues of the normal deoxynucleoside triphosphates are used as specific chain-terminating inhibitors of DNA polymerase. Single-stranded fragments obtained by nuclease action on the DNA are replicated by DNA polymerase I in the presence of a primer and a mixture of one dideoxynucleoside triphosphate and the four normal nucleoside triphosphates, one of which is labelled with ^{32}P. Separate incubations are carried out using analogous terminators for the other nucleotides. The effect is to yield radioactively-labelled stretches of DNA corresponding in length to the number of bases between the 5′ end and the position of the base corresponding to the terminator, which will be incorporated once into each stretch of DNA in such a way that it yields an appropriate stretch of DNA for every position occupied by the base in question. The resulting products from each incubation are separated in parallel by gel electrophoresis; from the pattern of radioactive bands obtained the sequence of the fragment can be read off. The method is reasonably accurate for sequences of 15 to about 200 nucleotides.

chair configuration (of a cyclobutadipyrimidine) *see* **pyrimidine dimer**.

chair conformation any **conformation** of a nonplanar, six-membered, saturated ring compound in which the ring atoms in relative positions 1, 2, 4, and 5 lie in one plane, and those in relative positions 3 and 6 lie on opposite sides of that plane. For a monosaccharide or monosaccharide derivative the conformational descriptor -*C* may be added to its name, and the reference plane is so chosen that the lowest-numbered carbon atom in the ring is exoplanar. See also $^1C_4$, $^4C_1$ *Compare* **boat conformation**.

chalcone **1** phenyl styryl ketone;1,3-diphenyl-2-propen-1-one. **2** any of a group of hydroxylated derivatives of chalcone (def. 1); they are important intermediates in plants in the biosynthesis of flavanones, flavones, flavonols, and anthocyanidins. The chalcone derivative **isoliquivitigenin** has anti-platelet activity, inhibiting 12-lipoxygenase. It stimulates soluble

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guanylate cyclase. It has anti-tumour activity and potently prevents tumour promotion by phorbol esters.

challenge **1** *(in immunology)* the act or process of injecting antigenic material into an immunized animal to test for immunity or to provoke a further immune response. **2** *(in endocrinology)* the act or process of administering an agent to evaluate hormonal responses. It is used to test hormonal control and function.

chalone any inhibitor affecting the cell cycle before the onset of mitosis that is tissue-specific and present in the tissue of action; it need not be species-specific. [From Greek *khalon*, to make slack.]

channel **1** a passage, often tubular or trough-shaped, along or through which movement of substances, especially fluids, can occur; e.g. a pore through a membrane. **2** the span between selected settings of two discriminators in a pulse counter, e.g. a scintillation counter, that defines the range of pulse intensities that will be recorded. **3** to guide into or cause to move through a particular channel or along a particular route; e.g. to channel a metabolite along a particular metabolic pathway. **4** descriptive of a membrane protein that transports ions across the membrane in the direction of the concentration gradient. *See also* **calcium channel**, **potassium channel**, **sodium channel**. — **channelled** *or* (*US*) **channeled** *adj.*

channel carrier *see* **ionophore**.

channel-forming integral membrane protein 28 *abbr.*: CHIP 28; *other name*: aquaporin 1; an integral membrane protein that forms a water-specific channel that provides the plasma membranes of red cells and kidney proximal tubules with high permeability to water. It is a homotetramer. Example from human: database code AQP1_HUMAN, 269 amino acids (28.49 kDa).

channelling *or* (*US*) **channeling** (*in column chromatography*) the uneven flow resulting from inhomogeneous packing of the column.

channel protein an **integral (cell membrane) protein** that permits the controlled (gated) movement of ions through a membrane. *See* **calcium channel**, **potassium channel**, **sodium channel**.

channels-ratio method a method of quench correcting in liquid scintillation counting in which two channels are used to measure the average energies of beta particles both before and after quenching.

chaoptin an extracellular membrane glycoprotein required for *Drosophila melanogaster* photoreceptor cell morphogenesis and containing a **leucine-rich repeat** domain. It is a cell-type specific adhesion molecule, exclusively localized to photoreceptor cells, linked to the outer surface of the membrane by a **GPI-anchor**. Example (precursor) from *D. melanogaster*: database code CHAO_DROME, 1134 amino acids (130.57 kDa).

Chaotropase *the proprietary name for* a mixture of endopeptidases isolated from *Streptomyces griseus*, so named for their stability and activity in the presence of the **chaotrope** 6 M guanidinium chloride.

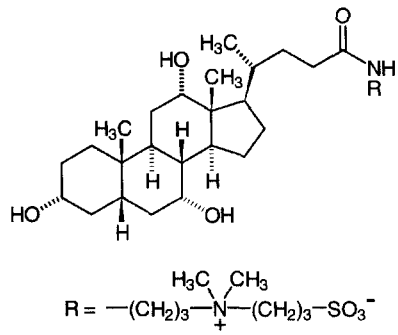
chaotrope *or* **chaotropic agent** any substance that increases the transfer of apolar groups to water because of its ability to decrease the 'ordered' structure of water and to increase its lipophilicity. Chaotropes are usually ions, e.g. SCN^-, CNS^-, ClO_4^-, I^-, Br^-, CH_3–COO^-. They cause the dissolution of biological membranes, the solubilization of particulate proteins, changes in the secondary, tertiary, and quaternary structure of proteins, and denaturation of nucleic acids.

chaotropic dissociation assay a technique used to measure the heterogeneity of antibody affinities in, e.g., serum. Immune complexes are dissociated in buffers of varying strengths and pH or in chaotropic agents (*see* **chaotrope**). Low-affinity antibodies dissociate more readily.

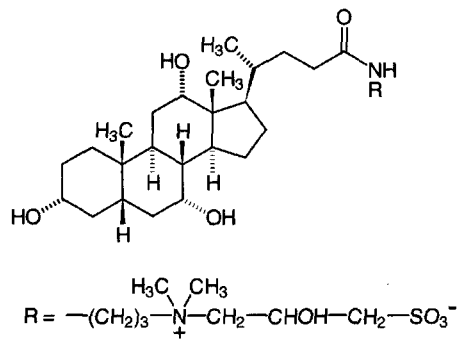
chaperone any of a functional class of unrelated families of proteins that assist the correct non-covalent assembly of other polypeptide-containing structures *in vivo*, but are not components of these assembled structures when they are performing their normal biological functions. *See also* **chaperonin**, **heat-shock protein**.

chaperonin any of a ubiquitous subclass of molecular **chaperones** implicated in the folding of other proteins. They include two kinds of proteins: (1) chaperonin 60 kDa (*also called* chaperonin-60 *or* cpn 60; the counterpart in other structures of the product of the ***groEL*** gene of *Escherichia coli*); five motifs identify such chaperonins; example from *Brassica napus*, plastid chaperonin-60: database code BNA60CPNA, 546 amino acids (57.63 kDa); and (2) chaperonin 10 kDa (*also called* chaperonin-10 *or* cpn 10; the counterpart in, e.g., *Mycobacterium* of the product of the ***groES*** gene of *E. coli*). *See also* **heat-shock protein**.

CHAPS 3-[(3-cholamidopropyl)dimethylammonio]-1-propanesulfonate; a zwitterionic detergent combining the properties of sulfobetaine and bile-salt types of detergent. It is used for membrane solubilization. Aggregation number 4–14, CMC 6–10 mM.



CHAPSO 3-[(3-cholamidopropyl)dimethylammonio]-2-hydroxy-1-propanesulfonate; zwitterionic detergent combining the properties of sulfobetaine and **bile-salt** types of detergent; it is more soluble than **CHAPS**. Aggregation number 11, CMC 8 mM.



characteristic group *(in chemistry)* any atom or group that is incorporated into a parent compound otherwise than by a direct carbon–carbon linkage, but including the groups –C=N and =C=X where X is O, S, Se, Te, NH, or substituted NH.

characteristic time a measure of the time required for a system to change from one state of motion to another, usually taken as the time required for the system to approach within one half of the new state of motion.

characteristic X-ray *see* **X-rays**.

Charcot–Marie–Tooth disease *see* **myelin proteins**.

Chargaff's rules a set of quantitative rules describing the base composition of duplex DNA: (1) [A] = [T] and (2) [G] = [C], where the square brackets denote the concentrations of the

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bases in moles per cent; minor bases, if present, are included with the appropriate major base. Three corollaries follow: (1) [A]/[T] = [G]/[C]; (2) total purines = total pyrimidines, i.e. [A] + [G] = [C] + [T]; and (3) total 6-aminobases = total 6-ketobases, [A] + [C] = [G] + [T]. A further consequence of these relationships is that the [A + T]/[G + C] ratio is a characteristic property of individual DNAs. [After Erwin Chargaff (1905–), US biochemist.]

charge **1** to load with the proper or appropriate quantity, e.g. to charge a tRNA molecule with an aminoacyl group, or to charge (an accumulator, capacitor, etc.) with electricity. **2** *see* **electric charge**. **3** the quantity of electricity held in, e.g., an accumulator or a capacitor. **4** a load. *Compare* **discharge**.

charge density *symbol* ρ; SI unit C m^{-3} (coulombs m^{-3}).

charged tRNA any **aminoacyl-tRNA** molecule.

charge-relay system a catalytic triad found in the serine proteases comprising, in chymotrypsin, the residues His^{57}, Ser^{195}, and Asp^{102}, the histidine being hydrogen bonded to the carboxylate of the buried aspartate. Spatially, these residues occur in positions such that the electronegativity of the aspartate carboxyl group can be relayed through the histidine nitrogen atoms to the serine hydroxyl group, enhancing its reactivity.

chargerin II *other names*: A61; protein 8 of H^+-transporting ATP synthase (EC 3.6.1.34); one of the chains of the nonenzymic component (CF_0 subunit) of the mitochondrial ATPase complex (membrane bound). Example from *Rattus norvegicus*: database code ATP8_RAT, 67 amino acids (7.63 kDa). *See also* **H^+-transporting ATP synthase**.

charge-shift electrophoresis a method of **electrophoresis** in a detergent solution in which the net charges of the complexes between amphiphilic proteins and the detergent depend on the charge of the latter, while the net charges on hydrophilic proteins are unaffected. This effect is exploited in, e.g., SDS–polyacrylamide gel electrophoresis.

charge-transfer chromatography a method of **liquid-gel chromatography** in which separation is due to electronic coupling between molecules being chromatographed and strong electron donor or acceptor groups attached to the supporting gel.

charge-transfer complex a complex that may be formed in an oxidation–reduction reaction, corresponding to electronic transition(s) to an excited state in which there is a partial transfer of electronic charge from the electron donor to the electron acceptor.

charging the covalent attachment of an aminoacyl group to a tRNA molecule to form an **aminoacyl-tRNA** molecule.

Charles's law *see* **gas laws**. [After Jacques Alexandre Cesar Charles (1746–1823), French physicist.]

charybdotoxin *abbr.*: ChTX; a 37-residue peptide isolated from the venom of the scorpion *Leiurus quinquestriatus hebraeus*. It is a potent inhibitor of some Ca^{2+}-activated K^+ channels and voltage-dependent K^+ channels, and probably acts at the outer face of the membrane, blocking the ion conductance channel. It has links between Cys residues 7–28, 13–33, and 17–35; amino-acid sequence:

XFTNVSCTTSKGCWSVCQRLHNTSR-
GKCMNKKCRCYS

(X = pyroglutamyl).

chase **1** the effective termination of incorporation of either a (radio)nuclide or a labelled compound into a substance, brought about by the addition of a large excess of an isotope of the (radio)nuclide or the unlabelled compound to the system, used especially after a pulse. **2** the quantity of isotope or unlabelled compound added to stop the incorporation of a (radio)nuclide or a labelled compound.

che the symbol for any of a class of genes that are implicated in chemotaxis in *Escherichia coli*. For example, *cheA* encodes a chemotaxis protein, protein phosphotransferase (EC 2.7.1.–), that is autophosphorylated and transfers its phosphate to CheB and CheC. Other two-component bacterial regulatory proteins are related. Example: database code CHEA_ECOLI, 654 amino acids (71.24 kDa). *cheB* encodes a chemotaxis protein, **protein-glutamate methylesterase** (EC 3.1.1.61), that catalyses the hydrolysis of protein L-glutamate *O*-methyl ester to protein L-glutamate and methanol. The protein is a **methyl-accepting chemotaxis protein** (MCP), the methylation state of which is crucial for sensory responses and adaptations. Example: database code CHEB_ECOLI, 349 amino acids (37.45 kDa). *cheR* encodes the chemotaxis protein methyltransferase (EC 2.1.1.80); it catalyses the reaction:

S-adenosyl-L-methionine + protein L-glutamate =
S-adenosyl-L-homocysteine + protein L-glutamate methyl ester.

The protein is an MCP, the methylation state of which is crucial for sensory responses and adaptations. Example: database code CHER_ECOLI, 286 amino acids (32.71 kDa). *cheW* encodes a purine-binding chemotaxis protein that is involved in the transmission of sensory signals from chemoreceptors to the flagellar motors. Example: database code CHEW_ECOLI, 167 amino acids (18.06 kDa). *cheY* encodes a chemotaxis protein involved in the transmission of sensory signals from chemoreceptors to flagellar motors and the regulation of clockwise rotation. Example: database code CHEY_ECOLI, 128 amino acids (13.95 kDa); the 3-D structure (NRL_3CHY) is known; the structure is largely α-helical, with some β-strands. *cheZ* encodes a chemotaxis protein thought to be involved in generating a regulating signal for bacterial flagellar rotation. Example: database code CHEZ_ECOLI, 214 amino acids (23.95 kDa).

checkpoint a point in the eukaryotic **cell division cycle** where the cycle can be halted until conditions are suitable for the cell to proceed to the next stage.

chel *abbr. for* chelate effect.

chelate **1** any chemical species in which there is **chelation**. **2** of, or denoting, a chelate (def. 1). **3** to form a chelate compound; to effect **chelation**. A chelate compound is a chemical compound in which a metal ion is combined with a substance that contains two or more electron donor groups so that the resulting structure contains one or more rings. —**chelated** *adj.*

chelate effect *abbr.*: chel; the stability difference between a chelate complex and the corresponding complex with simple ligands. For the displacement reaction:

$$MA_n + mL \rightarrow ML_m + nA,$$

$$\text{chel} = \log \beta_m (ML_m) - \log \beta_n (MA_n),$$

where ML_m and MA_n are complexes containing an equal number of the same donor atoms. Ligand L is multidentate, containing several donor atoms of the same element as the unidentate ligand A, and β_m and β_n are the overall stability constants.

chelating agent *or* **chelator** a substance that is able to form a **chelate compound** with a metal ion.

chelation the formation or presence of bonds from two or more atoms within the same ligand to a single central (metal) atom.

Chelex 100 *the proprietary name for* a synthetic ion-exchange resin consisting of a styrene divinylbenzene copolymer containing paired iminodiacetate groups that act as chelating groups in binding metal ions, especially transition-metal or other divalent ions.

chemical adsorption *an alternative term for* **chemisorption**.

chemical antagonism antagonism resulting from the chemical combination of an **antagonist** with the substance being antagonized.

chemical carcinogen any carcinogenic substance of low relative molecular mass. *See* **carcinogen**.

chemical cleavage method *or* **Maxam–Gilbert method** a rapid technique for determining nucleotide sequences in DNA (or in restriction fragments) that depends on labelling either end of a DNA strand with ^{32}P and the subsequent preferential, partial chemical cleavage of the labelled DNA specifically at

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positions occupied by one of the four possible bases. This results in a nested set of radioactive fragments extending from the ^{32}P label to each of the positions occupied by the particular base. The process is then repeated with cleavage, in turn, at each of the other three bases. The four sets of radioactive fragments are then separated, in adjacent lanes, by polyacrylamide gel electrophoresis, which arranges oligonucleotides in ascending order of the number of nucleotide residues contained. The base sequence of the original piece of DNA can be read directly from an autoradiograph of the resultant gel. The method can be used for sequences of 150 or more nucleotide residues. *Compare* **chain-termination method**. [After Allan M. Maxam and Walter Gilbert (1932–).]

chemical coupling hypothesis the hypothesis that the coupling of ATP synthesis to oxidation in oxidative phosphorylation is due to the formation of common 'high-energy' intermediates during electron transport that are subsequently used to phosphorylate ADP to ATP. It has been superseded by the **chemiosmotic coupling hypothesis**.

chemical equivalent the combining proportion of a substance, by mass, relative to a hydrogen standard. The chemical equivalent of an element is the number of grams of that element that will combine with or replace 1 g of hydrogen.

chemical exchange the changing magnetic environment of an atomic nucleus in a molecule that is rapidly undergoing reversible chemical or physical changes, which in turn produces changes in the **chemical shift** of that nucleus.

chemically induced dynamic nuclear polarization *abbr.*: CIDNP; a technique for the direct detection and identification of low concentrations of free radicals by **electron spin resonance**. It depends on strong polarization of certain nuclear spins by the unpaired electron during the molecule's existence as a free radical.

chemical messenger a term sometimes used loosely to mean variously a hormone, a neurocrine or paracrine transmitter, or a rheoseme. *See also* **second messenger**.

chemical oxygen demand *abbr.*: COD; a measure of the oxygen equivalent of that portion of the organic matter in a sample of water that is susceptible to oxidation by a strong chemical oxidant. Essentially the sample is boiled under a reflux condenser with potassium dichromate in strong sulfuric acid (with silver sulfate as catalyst); part of the dichromate is reduced by the contained organic matter and the remaining dichromate is titrated with ferrous sulfate. The result is expressed as milligrams oxygen absorbed from standard dichromate per litre of sample. *Compare* **biochemical oxygen demand**.

chemical pathology the branch of pathology dealing with the biochemistry of disease processes and the measurement of the amounts of substances present in body fluids and other samples as an aid to diagnosis.

chemical potential *symbol*: μ; the partial molar free energy of a chemical entity; the entity in question may be indicated by a subscript. For example, μ_B symbolizes the chemical potential of entity B in a mixture of entities B, C, ... etc. It is defined by:

$$\mu_B = (\partial G/\partial n_B)_{T,P,n_C},$$

where G is the Gibbs energy of the mixture, T is the thermodynamic temperature, P is the pressure, and n_B, n_C, ... etc. are the amounts of the entities B, C, ... etc. in the mixture.

chemical quenching *or* **impurity quenching** the **quenching** that occurs in liquid scintillation counting due to diffusion-controlled collisional interaction between the quencher molecules and the excited solvent and solute molecules. *Compare* **colour quenching**.

chemical reaction any single process or operation involving the interconversion of chemical species through changes in orbital electrons but not in the atomic nuclei.

chemical score a measure of the nutritional value of a protein. The limiting essential amino acid in the test protein is expressed as the percentage of the amount of the same amino acid present in egg albumin, the nutritionally perfect protein. Chemical score is numerically equal to **biological value**.

chemical shift the displacement of a resonance signal in NMR spectroscopy along the magnetic field coordinate resulting primarily from the magnetic effects of the chemical environment of the nuclei producing that signal. *See* **nuclear magnetic resonance**.

chemical species any set of chemically identical **molecular entities**, the members of which have the same composition and can explore the same set of molecular energy levels within the time scale of a particular experiment. Two conformational isomers may interconvert sufficiently slowly to be considered separate chemical species on an NMR time scale, but in a slow chemical reaction they may interconvert sufficiently quickly to be considered as a single chemical species.

chemical transmitter *(sometimes) an alternative term for* **neurotransmitter**.

chemiluminescence the production of visible light (luminescence) occurring as a result of a chemical reaction. It occurs, for example, during the **respiratory burst** in neutrophils and other phagocytic cells. The phenomenon is now exploited in sensitive enzyme assays and labelling methods in nucleic-acid hybridization, etc.

chemiosmotic coupling hypothesis a hypothesis proposed in 1961 by the British biochemist Peter Mitchell to explain ATP formation in mitochondria. Essentially it states that the energy-yielding reactions of the **respiratory chain** are coupled to the energy-requiring reactions of phosphorylation through the creation of a membrane electrochemical potential. An electrochemical gradient of H^+ ions, and a voltage gradient, is established across the mitochondrial inner membrane during electron flow through the respiratory chain. The electron carriers of the respiratory chain serve as an active-transport system or 'pump' to transport H^+ ions from the mitochondrial matrix across the inner membrane, which is an integral part of the coupling mechanism. The electrochemical gradient thus formed drives the synthesis of ATP from ADP and P_i. A similar mechanism is believed to drive oxidative phosphorylation in the chloroplast during the **light reactions of photosynthesis**.

chemism *(rare)* chemical action, operation, activity, or force.

chemisorption *or* **chemical adsorption** a type of **adsorption** in which the forces involved are valence forces of the same kind as those operating in the formation of chemical compounds. *Compare* **physisorption**.

chemoattractant *an alternative term for* **attractant**.

chemoautotroph *or* **chemolithotroph** any organism that is both an **autotroph** and a **chemotroph**. —**chemoautotrophic** *adj.*

chemoceptor *an alternative name for* **chemoreceptor** (esp. in immunology).

chemography an artefact in autoradiography due either to the creation of reduced crystals in the photographic emulsion by chemicals present in the specimen (**positive chemography**), or to the removal of latent images, also by chemicals in the specimen (**negative chemography**).

chemoheterotroph *or* **chemoorganotroph** any organism that is both a **chemotroph** and a **heterotroph**. —**chemoheterotrophic** *adj.*

chemokine *or* **intercrine** any of a subgroup of cytokines acting primarily on hemopoietic cells in acute and inflammatory processes and other immunoregulatory functions. They are chemotactic and related by primary structure, especially conservation of a motif of four cysteines, the first two of which are either adjacent or separated by one other residue.

chemolithotroph *an alternative term for* **chemoautotroph**.

chemoorganotroph *an alternative term for* **chemoheterotroph**.

chemoreceptor *or* **chemoceptor** any **receptor** on a cell that receives chemical stimuli and reacts to them or binds them.

chemostat a device for the continuous culture of bacterial (and other) cells. Growth occurs in an aerated fermenter vessel and its rate is controlled by the rate of addition of fresh nutrient from a reservoir (i.e. the dilution rate); this in turn controls the rate of removal of cells (and culture medium). In a

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chemostat, as opposed to an **auxostat**, the dilution rate is constant. At equilibrium, the rate of production of new cells by multiplication is equal to the rate of removal of grown cells.

chemosynthesis the synthesis of organic chemical compounds by an organism using energy obtained from the oxidation of inorganic chemical compounds rather than from light. *Compare* **photosynthesis**. —**chemosynthetic** *adj.*

chemotactic factor for macrophages *see* **lymphokine**.

chemotaxin *(sometimes) an alternative term for* **cytotaxin**.

chemotaxis **1** a movement of a motile cell or organism (*see* **taxis**) in response to a specific chemical concentration gradient. Movement may be towards a higher concentration (**positive chemotaxis**) or towards a lower concentration (**negative chemotaxis**). In *Escherichia coli* the ***che*** family of genes has been implicated in controlling certain aspects of chemotaxis, and **galactose/glucose binding protein** is also involved. *See also* **cytotaxis**. **2** *(in immunology)* the migration of polymorphonuclear leukocytes and macrophages towards higher concentrations of certain fragments of complement such as C3a and C5a. *See also* **lymphokine**. —**chemotactic** *adj.*

chemotaxonomy the classification of organisms on the basis of the nature, content, and/or the distribution of constituent chemical substances, e.g. DNA.

chemotherapy the treatment of disease, especially infections and neoplasms, with chemical agents (**chemotherapeutic agents**) that act specifically on infective organisms or tumours. The term also describes the treatment of psychiatric disease with chemical agents (as opposed to cognitive therapy). —**chemotherapeutic** *adj.*

chemotractant *see* **attractant**.

chemotroph any organism that derives its energy from exogenous chemical sources, independently of light. Chemotrophs may be subdivided into (1) chemoautotrophs (or chemolithotrophs) i.e. organisms that are both chemotrophs and **autotrophs** and (2) chemoheterotrophs (or chemoorganotrophs) i.e. organisms that are both chemotrophs and heterotrophs. *Compare* **phototroph**. —**chemotrophic** *adj.*; **chemotrophy** *n.*

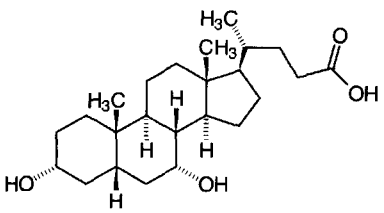
chemotropism the orientation of cells or organisms in response to chemical stimuli. The term is used especially of plants or plant organs. *See also* **tropism**. —**chemotropic** *adj.*

Cheng–Prussoff equation an equation relating the concentration, I_{50}, of a competitive ligand required to reduce the binding of a substrate to an enzyme by 50%, to the dissociation constant, K_i, of the enzyme–inhibitor complex; it is:

$$I_{50} = K_i\,(1 + S/K_m),$$

where S is the substrate concentration and K_m the Michaelis constant for the enzyme–substrate complex.

chenodeoxycholate *or* **chenodiol** the anion of (3α,5β,7α)-3,7-dihydroxycholan-24-oic acid; a major component of bile in some species (hens, geese) but a minor component in humans. It is used therapeutically to decrease the synthesis of cholesterol and to help dissolve cholesterol gallstones.

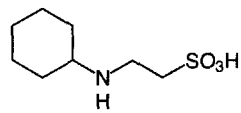


Cherenkov, Pavel Alekseyevich (1904–1990), Russian-born Soviet physicist noted for his study of the effects produced by high-energy charged particles; Nobel Laureate in Physics (1958) jointly with I. M. Frank and I. Y. Tamm 'for the discovery and interpretation of the Cherenkov effect'.

Cherenkov counter *or* **Cerenkov counter** a device for counting charged particles, or radionuclides emitting them, that depends on **Cherenkov radiation**.

Cherenkov radiation *or* **Cerenkov radiation** a radiation of bluish light, consisting of photons, emitted when charged particles, especially high-energy beta particles, pass through either a solid or liquid medium at velocities greater than that at which light passes through the same medium. The effect is analogous to the creation of a sonic boom that occurs when an object exceeds the speed of sound in a medium.

Ches *abbr. for* 2-(cyclohexylamino)ethanesulfonic acid; a compound with similar properties to a **Good buffer substance**; pK_a (25 °C) = 9.3.



chewing gum *see* **chicle**.

chi *symbol*: χ (lower case) *or* X (upper case); the twenty-second letter of the Greek alphabet. For uses *see* **Appendix A**.

chiasma (*pl.* **chiasmata**) **1** *(in genetics)* a connection formed between **chromatids**, visible during **meiosis**, thought to be the point of the interchange involved in crossing-over. **2** *or (esp. US)* **chiasm** (*pl.* **chiasms**) *(in anatomy)* a decussation or intersection, as of two nerves; e.g. optic chiasma.

chicle a mixture of *cis*- and *trans*-1,4-polyprenoids obtained from the evergreen tree, *Achras sapota*; the original chewing gum base.

chimera *or (esp. Brit.)* **chimaera** *(in genetics)* an organism comprising tissues of two or more **genotypes**. Chimeras can occur as a result of mutation, abnormal distribution of chromosomes, or grafting. *See* **mosaic**, **transgenic**, **chimeric molecule**. —**chimeric** *or* **chimaeric** *adj.*

chimeric molecule **1** any of the hybrid DNA molecules formed when DNAs from different sources are digested with the same **restriction endonuclease** and the digests are mixed. The DNA fragments in the mixture become associated by hydrogen bonds between complementary sequences to form new arrangements, which may be converted into covalently linked molecules by the action of DNA ligase. This process can produce **chimeric plasmids** and other chimeric structures. **2** a **chimeric protein** is a protein obtained by the insertion or substitution of a partial sequence from one protein into another, typically using cDNA technology. The resultant protein thus has elements of both the original proteins. **3** a recombinant antibody that has, e.g., structural characteristics of both human and mouse antibodies.

chimerin any of several related proteins that function as GTPase-activating proteins, specific for the p21 Ras-related Rac GTPase. They include n-chimerin, and α- and β-chimerins. n-Chimerin is a cerebellar protein and β-chimerin is expressed in testis. They are phorbol ester receptors, with an N-terminal domain homologous to the zinc-finger region of protein kinase C, and a C-terminal domain homologous to the product of ***BCR***. Through their action on Rac, they lead to changes in cytoskeletal organization. Example from human: database code A53764, 466 amino acids (53.81 kDa).

chimyl alcohol glycerol 1-hexadecyl ether, (+)-3-(hexadecyloxy)-1,2-propanediol; a hydrolysis product of **ether lipids**.

Chinese restaurant syndrome *see* **monosodium glutamate**.

CHIP 28 *abbr. for* channel-forming integral membrane protein 28.

chiral describing a chemical compound that displays **chirality**.

chiral drug a single pure enantiomer of a specified drug rather than the racemate; the enantiomers may have very different

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pharmacological effects, e.g. in the case of propoxyphene and levopropoxyphene.

chirality topological handedness; the property of nonidentity of an object with its mirror image. A chiral chemical compound, i.e. one that possesses chirality, is one that cannot be superimposed on its mirror image, either as a result of simple reflection or after rotation and reflection. If superposition can be achieved then the molecule is said to be **achiral**. Chirality is most commonly due to the presence of one or more **chiral centres** (formerly referred to as asymmetric carbon atoms) or the presence of a **chiral axis** (as in allene structures, some of which are found in natural products). Rarely, chirality may also result from the presence of a chiral plane. *See also* **prochiral**. [From Greek *kheir*, hand.]

chiral methyl a carbon atom carrying the three hydrogen isotopes, i.e. -$C^1H^2H^3H$.

chiral recognition the differentiation of the enantiomers of a compound. This can be achieved by living organisms, chiral molecules, enzymes, drug receptors, etc.

chiroid *(rare)* any molecule that has **chirality**.

chiroptical describing any of the phenomena that depend on the ability of chiral and other intrinsically asymmetric molecules to rotate the plane of polarized light, known collectively as **optical activity**. Such phenomena include **optical rotation**, **optical rotatory dispersion**, and **circular dichroism**. The term is also applied to any of the techniques used for investigating these phenomena.

chi sequence *or* **chi site** a sequence of base pairs first discovered in a phage lambda mutant, called *chi*. These mutants were found to have single base pair changes creating sites that stimulate **recombination**. Characteristic of chi sites is a nonsymmetrical sequence of eight base pairs, consensus sequence:

5′ GCTGGTGG 3′.

A recombinational hot spot in *Escherichia coli* and a binding site for **Rec A** is a chi site.

chi site *see* **chi sequence**.

chi-square test a statistical test to determine whether an observed series of values differs from a series of values expected on a hypothesis, to a greater degree than would be expected by chance. If m is the expected value and $(m + x)$ is the observed value then $\chi^2 = \Sigma(x^2/m)$. The goodness of fit may be found from available tables of χ^2 and the number of degrees of freedom, n, in which the observed series may differ from the hypothetical.

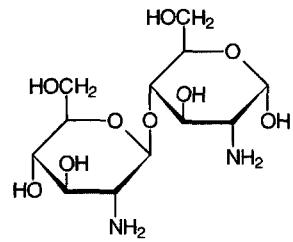
chi structure a structure formed when circular duplex DNA that is undergoing **recombination** is cut with a restriction enzyme. This yields two strands joined at a site intermediate between the ends, which by electron microscopy can yield a shape with the appearance of the Greek letter χ. The structure results from the fact that if two circular duplex DNAs undergo site-specific recombination, a single strand from each duplex will be opened and the two single strands ligated to each other to form a figure of eight. If each of the loops of this figure of eight is cut by the restriction enzyme the chi structure will result. *Compare* **Holliday junction**.

chitin a linear polysaccharide consisting of β-1,4-linked *N*-acetyl-D-glucosamine residues. It is found in annelid cuticle, arthropod exoskeleton, and in some plants and fungi. In fungi, chitin represents the microfibrillar component of the cell wall. *See also* **chitobiose**, **chitosan**.

chitinase EC 3.2.1.14; *other names*: chitodextrinase; 1,4-β-poly-*N*-acetylglucosaminidase; poly-β-glucosaminidase. An enzyme that catalyses the hydrolysis of the 1,4-β-linkages of *N*-acetyl-D-glucosamine polymers of chitin. Example, endochitinase from *Hordeum vulgare* (barley): database code NRL_1BAA, 243 amino acids (25.92 kDa); 3-D structure known, largely α helix.

chitin synthase EC 2.4.1.16; *other name*: chitin–UDP *N*-acetyl-glucosaminyltransferase; an enzyme that catalyses the reaction between UDP-*N*-acetyl-D-glucosamine and [1,4-(*N*-acetyl-β-D-glucosaminyl)]$_n$ to form UDP and[1,4-(*N*-acetyl-β-D-glucosaminyl)]$_{n+1}$. Example from *Neurospora crassa*: database code CHS3_NEUCR, 960 amino acids (106.78 kDa).

chitobiose 4-*O*-(2-amino-2-deoxy-β-D-glucopyranosyl)-2-amino-2-deoxy-D-glucose; *condensed form*: Glc*p*N(β1-4)GlcN; a disaccharide found in its acetylated form in chitin. This acetylated form, Glc*p*NAc(β1-4)GlcNAc, is the repeating unit of chitin, and should, logically, have the name chitobiose (by analogy with cellobiose, the repeating unit of cellulose). However, historically the nonacetylated form received the name chitobiose, a convention that has persisted.



α-anomer

chitosamine *see* **glucosamine**.

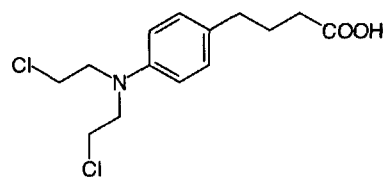
chitosan the cationic polymeric carbohydrate obtained by the deacetylation of **chitin**.

chitosome a body found in fungi and containing chitin synthase; it synthesizes chitin microfibrils.

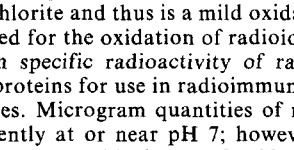
Chl *abbr. for* chlorophyll.

chlor+ *a variant of* **chloro+** (sometimes before a vowel).

chlorambucil 4-[bis(2-chloroethyl)amino]benzenebutanoic acid; an alkylating agent that reacts with DNA causing the formation of covalent bonds that cross-link with the two strands of DNA, thereby preventing its replication.



chloramine T *N*-chloro-4-methylbenzenesulfonamide sodium salt; sodium 4-toluenesulfonchloramide hydrate; CH_3–C_6H_4–$SO_2NClNa{\cdot}xH_2O$. A white crystalline solid with a faint odour of chlorine. In aqueous solution it slowly decomposes to sodium hypochlorite and thus is a mild oxidant and antiseptic. It is widely used for the oxidation of radioiodide in the preparation at high specific radioactivity of radioiodine-labelled peptides and proteins for use in radioimmunoassay or other *in vitro* techniques. Microgram quantities of many proteins are labelled efficiently at or near pH 7; however, some proteins may suffer an unacceptable degree of oxidative damage.



chloramphenicol *abbr.*: CAP; a broad-spectrum, chlorine-containing antibiotic produced by *Streptomyces venezuelae*; it

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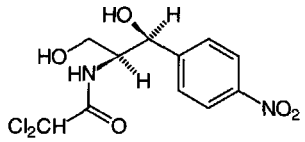
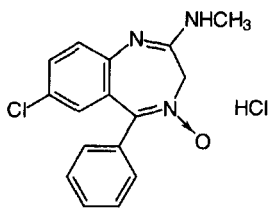
is now produced by chemical synthesis. The configurations at C-1 and C-2 are (*S*), as shown in the structure. It inhibits prokaryotic protein synthesis by attaching to the 50S ribosomal subunit and inhibiting peptidyltransferase (EC 2.3.2.12), thereby preventing the formation of peptide bonds. Chloramphenicol also inhibits protein synthesis in mitochondria, and this accounts for its toxic effect in causing aplastic anemia. It is much used for the treatment of typhoid fever.



chloramphenicol *O*-acetyltransferase *abbr.*: CAT; EC 2.3.1.28; a bacterial enzyme, not found in eukaryotes, that catalyses the reaction between acetyl-CoA and chloramphenicol to form CoA and chloramphenicol 3-acetate. This reaction forms the basis for acquired chloramphenicol resistance in certain bacterial strains. Also the gene for CAT is used as a **reporter** because its expression can be detected by a sensitive radiochemical assay. In cDNA technology, for example, the expression of a eukaryotic promoter can be characterized by assay of the enzyme if CAT cDNA is included in the genes to be expressed. Example from *Escherichia coli*: database code CAT2_ECOLI, 213 amino acids (24.75 kDa).

chlordiazepoxide 7-chloro-*N*-methyl-5-phenyl-3*H*-1,4-benzodiazepin-2-amine 4-oxide; a CNS depressant noted primarily for its effective anti-anxiety effects at nonsedative doses. It is the prototypical **benzodiazepine**, used therapeutically as the hydrochloride. It is a controlled substance in the US Code of Federal Regulations. One proprietary name of the hydrochloride is Librium.



chloride **1** *symbol*: Cl^-; the anion of the element chlorine. **2** any salt of hydrochloric acid. **3** any compound containing a chlorine atom in organic linkage.

chloride channel any of a family of proteins that facilitate Cl^- transport through a membrane. These channels are of two types: (1) ligand-gated Cl^- channels associated with inhibitory neurotransmitter receptors such as the **GABA receptor** or the **glycine receptor**; and (2) voltage-gated Cl^- channels. These have 13 transmembrane helical regions, the last two being separated by a long (between 130 and 160 residue) cytoplasmic loop. In nerve membranes these channels ensure the high conductance of non-innervated membranes of the electrolyte necessary for efficient current generation caused by Na^+ influx through the acetylcholine receptor at the innervated membrane. Example from *Torpedo californica*: database code CICH_TORCA, 810 amino acids (89.45 kDa). In muscle cells voltage-gated Cl^- channels are involved in regulation of cell volume, membrane potential stabilization, and transepithelial transport. Examples: database code CIC1_HUMAN, 988 amino acids (108.74 kDa). A Cl^- channel in the kidney proximal tubule is involved in chloride reabsorption. Example from *Rattus norvegicus*: database code CICK_RAT, 686 amino acids (75.63 kDa). *See also* **cystic fibrosis transmembrane conductance regulator**.

chloride shift *or* **Hamberger shift** the phenomenon whereby, because of the **isohydric shift**, there is a higher concentration of hydrogencarbonate ions in the erythrocytes in blood leaving the tissues (venous blood) than in arterial blood, and hence the hydrogencarbonate/chloride ion ratio is higher in the erythrocytes than in plasma. This results in a movement of hydrogencarbonate ions out of the erythrocytes into the plasma and an equivalent movement of chloride ions from the plasma into the erythrocytes. In the lungs the reverse ion movements occur upon the oxygenation (arterialization) of the blood there.

chlorin *a trivial name for* 2,3-dihydroporphyrin.

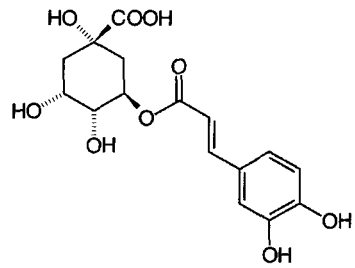
chlorinate **1** to treat or react (a substance) with dichlorine. **2** to introduce one or more chloro groups into an organic compound, whether by addition or substitution. **3** to disinfect (especially water) with dichlorine. —**chlorination** *n.*

chlorine **1** *symbol*: Cl; a halogen element of group 17 of the IUPAC **periodic table**; atomic number 17; relative atomic mass 35.453. The 15th most abundant element of the Earth's crust, occurring in the combined state, mostly as inorganic chlorides. **2** *symbol*: Cl_2; the common name for the yellowish-green gaseous substance, correctly known as **dichlorine**.

chloro+ *or (sometimes before a vowel)* **chlor+** *comb. form* **1** denoting a chlorine atom in organic linkage. **2** denoting the colour green.

chlorocruorin any green, approximately 3 MDa, hemochrome respiratory pigment found in the blood of certain polychaete annelids; it contains 96 heme groups.

chlorogenic acid 3-*O*-(3,4-dihydroxycinnamoyl)-D-quinic acid; a tannin found in tea and coffee.



chlorolabe a pigment sensitive to green light (535 nm) found in some retinal cones. It is lacking in subjects with green-blindness but present in those with red-blindness. *Compare* **cyanolabe**, **erythrolabe**.

***p*-chloromercuribenzenesulfonate** *abbr.*: PCMBS; 4-(chloromercuri)benzenesulfonate; $Cl–Hg–C_6H_4–SO_3^-$; a reagent that reacts with thiol groups; it is more soluble than *p*-chloromercuribenzoate.

***p*-chloromercuribenzoate** *abbr.*: PCMB; 4-(chloromercuri)-benzoate; $Cl–Hg–C_6H_4–COO^-$; a reagent that reacts with thiol groups. It is supplied either as *p*-chloromercuribenzoic acid or as *p*-hydroxymercuribenzoate sodium salt.

4-chloromercuriphenylsulfonate *see* ***p*-chloromercuribenzenesulfonate**.

chloroperoxidase EC 1.11.1.10; *other name*: chloride peroxidase. An enzyme that catalyses a reaction between H_2O_2, two molecules of Cl^- ion, and two molecules of an organic compound to form two molecules of an organic chloride and two molecules of H_2O. It is useful for the introduction of (radioisotopes of) chlorine, bromine, or iodine into tyrosine residues in proteins. It is involved in the synthesis of chlorine-containing compounds such as (1*S-trans*)-2,2-dichloro-1,3-cyclopentanedione (caldariomycin). Example (precursor) from

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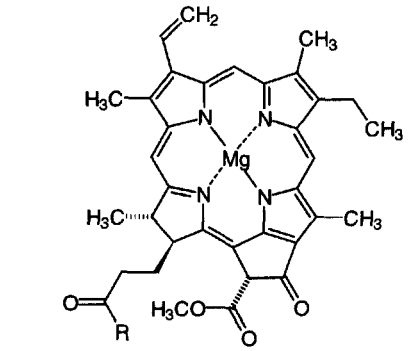
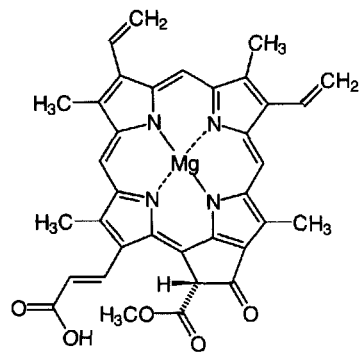
Caldariomyces fumago: database code PRXC_CALFU, 321 amino acids (35.20 kDa).

p′-chloro-p-phenylaniline *see* **4-amino-4′-chlorodiphenyl**.

chlorophyll any of the several green (or purple, *see* **bacteriochlorophyll**) pigments, found in plants and photosynthetic bacteria, that function in **photosynthesis** by absorbing light energy mainly in the red and violet-blue parts of the spectrum. Chlorophylls are magnesium complexes of various closely related porphyrins or chlorins. The main chlorophylls of land plants are chlorophylls *a* and *b*, and some algae contain chlorophylls *c*. Chlorophylls *a* and *b* are dihydroporphyrins, having no double bond at position 3 of ring B, while chlorophylls *c* are porphyrins. Photosynthetic bacteria contain various bacteriochlorophylls. The structure of chlorophyll *a* is shown. Chlorophyll *b* differs from chlorophyll *a* only in the presence of a formyl group in place of the methyl group at position 3 on ring B (Fischer system: *see* **bacteriochlorophyll**). Several chlorophylls *c* are known. They are accessory light-harvesting pigments found in eukaryotic algae that do not contain chlorophyll *b*. The structure of chlorophyll c_2 is shown, chlorophyll c_1 differing from this in having an ethyl group at position 4 of ring B, and chlorophyll c_3 differing from it in having a methylformyl group at position 3 of ring B. Most chlorophylls exist in **antenna complexes**, where their function is to absorb visible light and to transmit the energy so absorbed to a reaction centre in which other chlorophyll molecules are excited by the accumulated energy to transfer an electron to an electron transfer system known as a **photosystem**. Differences in structure have significant effects on the absorption spectrum of the chlorophyll molecule, i.e. on the wavelength of the light absorbed, and thus on the energy available as a result of the absorption (*see* **Planck constant** for the relationship). To restore its electronic state, the oxidized chlorophyll molecule can accept an electron from a water molecule (or, in photosynthetic sulfur bacteria, from hydrogen sulfide), the transfer being catalysed by a manganese-rich protein complex that is part of the photosystem. This reaction is responsible for the dioxygen (or sulfur) that is formed during photosynthesis, one molecule of dioxygen, four protons, and four electrons being produced from two water molecules. *See also* **P680**, **P690**, **P700**. [From the Greek *khloros*, yellowish or pale green, and *phyllon*, leaf.]

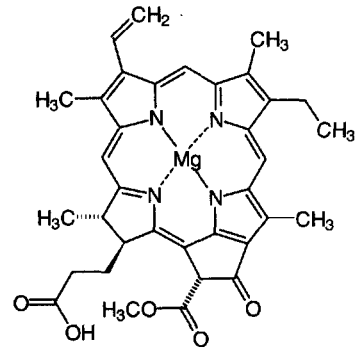


chlorophyll *a*



chlorophyll c_2

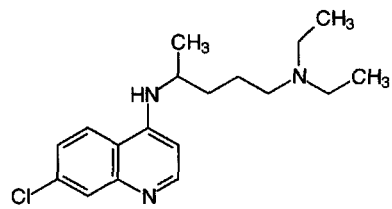
chlorophyllide a **chlorophyll** lacking the terpenoid side chain, usually phytol. The penultimate intermediate in chlorophyll biosynthesis. It is formed by the light-catalysed reduction of protochlorophyllide attached to a protein, protochlorophyllide holochrome.



chlorophyllide *a*

chloroplast *or (sometimes)* **chloroplastid** a chlorophyll-containing **plastid**, found in cells of algae and higher plants, that is the site of **photosynthesis**. Chloroplasts are characterized by a system of membranes embedded in a hydrophobic proteinaceous matrix, or stroma. The basic unit of the membrane system is a flattened single vesicle called the **thylakoid**; thylakoids stack into grana (*sing.* **granum**). All the thylakoids of a granum are connected with each other, and the grana are connected by intergranal lamellae.

chloroquine [N^4-(7-chloro-4-quinolinyl)-N^1,N^1-diethyl-1,4-pentanediamine; a widely used synthetic quinoline antimalarial drug, with action similar to **quinine**. It accumulates in the cells of the malaria parasites and prevents digestion of their host's hemoglobin; it may also possibly disrupt the parasite's ribonucleotide metabolism. *See also* **acridine**.



chlorosome a small compartment found in photosynthetic

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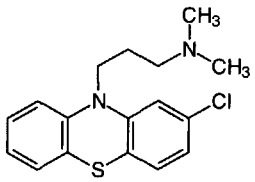
Chlorobiaceae bacteria. It contains **bacteriochlorophyll** *c* and is attached to the cytoplasmic membrane.

chlorosulfolipid a class of **sulfolipid** found in the alga, *Ochramonas danica*. They are based on *n*-docosane-1,14-diol disulfate; chlorine atoms have been located at C-2, C-13, C-15, and C-16.

chlorpromazine 2-chloro-10-(3-dimethylaminopropyl)phenothiazine; a **neuroleptic** drug with sedative and antiemetic actions. It acts as an antagonist at dopaminergic (D_2), α-adrenergic, and many other receptors (*see* **adrenoceptor**). It was formerly classed as a **major tranquillizer**, a term now deprecated. Largactil is one proprietary name of the hydrochloride.

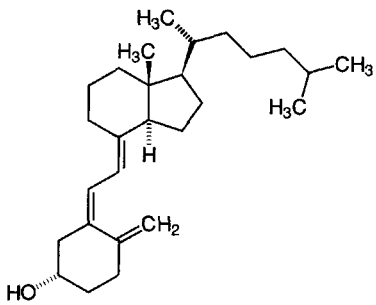


Cho *symbol for* a residue of choline.

CHO *abbr. for* Chinese hamster ovary (applied to cell cultures derived from this organ).

chole+ *or (before a vowel)* **chol+** *comb. form* denoting bile.

cholecalciferol *or* **calciol** *the recommended trivial name for* vitamin D_3; (5*Z*,7*E*)-(3*S*)-9,10-seco-5,7,10(19)-cholestatrien-3-ol. It is formed in skin by UV-irradiation of 7-dehydrocholesterol, and is metabolized to 1α,25-dihydroxycholecalciferol (calcitriol). The latter affects the absorption of calcium from the gastrointestinal tract and the metabolism of calcium in bone. *See* **vitamin D**.



cholecalcin an intracellular calcium-binding protein.

cholecystokinin *abbr.*: CCK; *formerly called* cholecystokinin–pancreozymin (*abbr.*: CCK-PZ); gall-bladder emptying peptide hormone from **I cells** of the duodenum and proximal jejunum of mammals, also present in most parts of the brain and in the nerves of the colon, ileum, and pancreas. It is identical with **pancreozymin**, the different names relating to the activities by which they were separately identified. The sequence of human cholecystokinin is

KAPSGRMSIVKNLQNLDPSHRISDRDY(-SO_3)-MGWMDF-NH_2.

Sulfation of the tyrosine is essential for activity. Highly heterogeneous, the various species are known by the number of amino-acid residues they contain, e.g. CCK-39, CCK-33 (e.g. human), CCK-12, CCK-8, CCK-4, etc.; all are truncated from the N terminus and thus contain the same C-terminal tetrapeptide amide sequence, which is identical to that of **gastrin** and in which the functional activity of gastrin largely resides. CCK is released when fat, peptones, amino acids, or $MgSO_4$ are placed on the intestinal mucosa; it causes contraction of the gall bladder and secretion of enzyme precursors from pancreatic acinar tissue, it appears to act as a neurotransmitter in a number of situations, and it elicits the behavioural sequence characteristic of satiety.

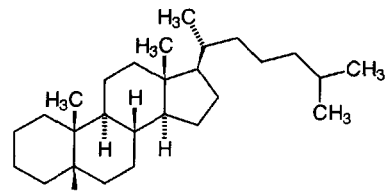
cholecystokinin receptor any of several membrane proteins that bind **cholecystokinin** forms and mediate their intracellular effects. Two types are recognized, designated CCK_A and CCK_B. Both types also bind gastrin, but type A binds cholecystokinin with 1000-fold higher affinity than gastrin. When CCK-8 and CCK-4 are used as agonists, CCK-8 is the most potent. Gastrin and CCK-4 are about equipotent, with much greater effect on CCK_B than CCK_A. CCK_B is regarded as the gastrin receptor. Both types of receptor are seven-transmembrane-segment receptors, coupled to G-proteins that stimulate the **phosphatidylinositol cycle**. Examples, human (precursors), type A: database code CCKR_HUMAN, 428 amino acids (47.84 kDa); type B: database code GASR_HUMAN, 447 amino acids (48.42 kDa).

choleragen *(sometimes) an alternative name for* **cholera toxin**.

choleragenoid a 57 kDa protein that occurs naturally in the cell-free culture fluid of *Vibrio cholerae* and is immunologically almost indistinguishable from **cholera toxin** but is non-toxic. It consists of the pentamer of the B subunit of the toxin without its A subunit.

cholera toxin *or* **choleragen** the antigenic and potently diarrheagenic **enterotoxin** produced by the cholera bacterium, *Vibrio cholerae*. Pathogenic strains of the bacterium secrete the toxin into their growth medium. The toxin is an 84 kDa multimeric protein of exceptional stability and formed of two dissimilar subunits: the A subunit consists of two polypeptide chains (α, 22 kDa; γ, 5 kDa) linked by a single disulfide bond; the B subunit consists of four to six noncovalently associated β chains (11.5 kDa each). Binding of the toxin to its receptor ganglioside (G_{M1}) in the membranes of sensitive cells occurs via the B subunit; the A subunit then activates cellular adenylate cyclase; together with cellular **ADP-ribosylation factor** it constitutes an **ADP-ribosyltransferase**, which transfers ADP-ribose to the **G-protein** α_s subunit, inhibiting its GTPase and converting it to an irreversible activator of adenylate cyclase. Database code CHTA_VIBCH, 258 amino acids (29.30 kDa), is precursor for chains α (amino acids 19–211) and γ (amino acids 213–258); database code CHTB_VIBCH, 124 amino acids (13.94 kDa), is precursor for β chain (signal is amino acids 1–21).

cholestane the fully saturated carbon skeleton from which **cholesterol** is structurally derived; the configuration at C-5 can be *α* or *β*; 5*β*-cholestane is known as **coprostane**.



5*β*-cholestane

cholestanol 3*β*,5*α*-cholestan-3-ol; dihydrocholesterol; 3*β*-hydroxycholestane; a steroid that occurs in human feces, gallstones, and in eggs.

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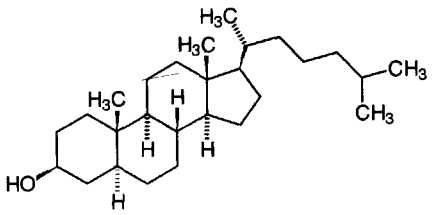
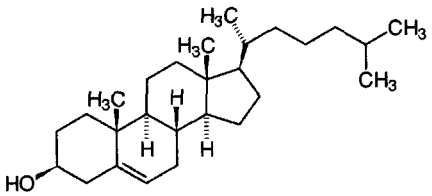


cholestanol

cholestasis the arrest (stasis) or impairment of bile flow. It may originate intrahepatically, due to hepatocellular defects, or extrahepatically, often due to obstruction of the bile duct by calculi.

cholesteric of, relating to, or resembling cholesterol or a derivative of cholesterol. *See also* **liquid crystal**.

cholesterol cholest-5-en-3β-ol; the principal sterol of vertebrates and the precursor of many steroids, including bile acids and steroid hormones. It is found in all animal tissues, especially brain and spinal cord, in the bile, and in gallstones, being a component of the plasma membrane lipid bilayer. It is also a component of the plasma lipoproteins and excessive levels in the plasma have been implicated in atherogenesis. It is synthesized from acetyl-CoA via hydroxymethylglutaryl-CoA and squalene.



cholesterol acyltransferase *see* **sterol *O*-acyltransferase**.

cholesterol desmolase *see* **cholesterol monooxygenase**.

cholesterol 7α-hydroxylase *see* **cholesterol 7α-monooxygenase**.

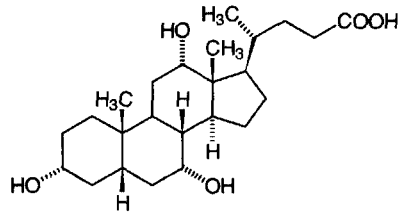
cholesterol 7α-monooxygenase EC 1.14.13.17; *other names*: cholesterol 7α-hydroxylase; cytochrome P450 VII; a cytochrome P450 enzyme that catalyses the hydroxylation of cholesterol to form 7α-cholesterol. NADPH and dioxygen are reactants, $NADP^+$ and H_2O being formed. This is the first step in the biosynthesis of bile acids from cholesterol and is rate-limiting. Example from human: database code CP70_HUMAN, 504 amino acids (57.66 kDa).

cholesterol monooxygenase (side-chain cleaving) EC 1.14.15.6; *systematic name*: cholesterol,reduced-adrenal-ferredoxin:oxygen oxidoreductase (side-chain-cleaving); *other names*: CYPXIA1 cholesterol desmolase; cholesterol side-chain cleavage enzyme; cytochrome $P450_{scc}$; a cytochrome P450 enzyme that catalyses the formation of pregnenolone from cholesterol, with release of 4-methylpentanal and H_2O. It is the first enzyme in the pathway for the biosynthesis of steroid hormones from cholesterol and is a rate-limiting step. It is a target for regulatory systems that stimulate steroid hormone biosynthesis. The reaction involves an oxidation by dioxygen, reduced adrenal ferredoxin being oxidized in the process. This is a heme-thiolate enzyme. Example from human: database code CPM1_HUMAN, 521 amino acids (60.11 kDa); a theoretical 3-D model for the bovine enzyme has been produced: database code NRL_1SCC, 482 amino acids (56.46 kDa).

cholesterol side-chain cleavage enzyme *see* **cholesterol monooxygenase (side-chain cleaving)**.

cholestyramine resin *see* **colestyramine resin**.

cholic acid 3α,7α,12α-trihydroxy-5β-cholan-24-oic acid; a metabolic derivative of cholesterol, produced in the liver and secreted as a **bile acid**. It is used as a detergent, as the sodium salt; aggregation number 2, CMC 9–15 mM.



choline *symbol*: Cho; *abbr.*: Ch; *N*,*N*,*N*-trimethylethanolammonium (ion); 2-hydroxyethyltrimethylammonium (ion); 2-hydroxy-*N*,*N*,*N*-trimethylethanaminium; $(CH_3)_3N^+–CH_2–CH_2–OH$. An amino alcohol that functions as a methyl group donor in metabolism; it also occurs in the neurotransmitter acetylcholine and in some phospholipids.

choline acetyltransferase EC 2.3.1.6; *recommended name*: choline *O*-acetyltransferase; *systematic name*: acetyl-CoA: choline *O*-acetyltransferase. An enzyme that catalyses the reaction between acetyl-CoA and choline to form *O*-acetylcholine and CoA. It is instrumental in the synthesis of the neurotransmitter acetylcholine. Example from rat: database code A48319, 644 amino acids (72.32 kDa). *See also* **cholinoceptor**.

choline kinase EC 2.7.1.32; an enzyme that catalyses the phosphorylation by ATP of choline to form *O*-phosphocholine and ADP. Phosphocholine (choline phosphate) is an important intermediate in phospholipid biosynthesis, reacting with CTP to form CDPcholine. Example from human: database code S23104, 456 amino acids (52.01 kDa). *See also* **choline-phosphate cytidylyltransferase**.

choline-phosphate cytidylyltransferase EC 2.7.7.15; *systematic name*: CTP:choline-phosphate cytidylyltransferase; *other name*: phosphorylcholine transferase. An enzyme that catalyses the formation of **cytidine(5′)diphosphocholine** (CDP-choline) from CTP and choline phosphate with release of pyrophosphate. Example from yeast: database code CTPT_YEAST, 424 amino acids (49.33 kDa).

cholinergic describing nerve fibres that, when activated, release acetylcholine or an acetylcholine-like substance from their endings. *Compare* **adrenergic**, **peptidergic**, **purinergic**. *See also* **cholinoceptor**.

cholinesterase **1** *recommended name for* EC 3.1.1.8; *other names*: choline esterase II, pseudocholinesterase. An enzyme that hydrolyses a variety of choline esters to choline and a carboxylic acid. In mammals, the enzyme is found in the liver, pancreas, heart, serum, and the white matter of brain. Its function is unknown. In humans, individuals with abnormally low activity of cholinesterase fail to hydrolyse succinylcholine, often given as a muscle relaxant in anaesthesia. The gene (E_1) encoding the enzyme can exist in at least four allelic forms, the normal (E_1^u), and three variants, E_1^a (atypical), E_1^f (fluoride resistant), and E_1^s (silent). Homozygotes for the atypical gene have a dibucaine-resistant enzyme which is weakly active against most enzyme substrates, and homozygotes for the silent gene exhibit minimal enzyme activity. Individuals having low enzyme activity from whatever cause may suffer prolonged respiratory paralysis after succinylcholine has been administered. Example from *Canis familiaris*: database code CHLE_CANFA, 141 amino acids (15.09 kDa). **2** alternative name for **acetylcholinesterase**.

cholinoceptor any receptor for acetylcholine on cholinergic or

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other neurons; such receptors occur on the postjunctional membrane of synaptic clefts or on terminal axons and mediate the neurotransmitter action of acetylcholine. Cholinoceptors may be divided into two main types: (1) **muscarinic cholinoceptors** of smooth muscle, cardiac muscle, endocrine glands, and the central nervous system at which muscarine, but not nicotine, can readily mimic the action of acetylcholine; and (2) **nicotinic cholinoceptors** of skeletal muscle, ganglia, and the central nervous system at which nicotine, but not muscarine, can readily mimic the action of acetylcholine.

Muscarinic acetylcholine receptors for which structures are known are all G-protein-coupled and of the single polypeptide chain, seven-transmembrane-helix class. They fall into five types: four are designated M_1–M_4; a fifth, which has been cloned, acts through phosphoinositide-specific phospholipase C when expressed in CHO cells, but although mRNA has been isolated from brain, a translation product has not been found *in vivo*; its database code is ACM5_HUMAN, 532 amino acids (60.00 kDa). Of the remainder, M_1 (database code, human, ACM1_HUMAN, 460 amino acids (51.36 kDa)) and M_3 (database code, human, ACM3_HUMAN, 590 amino acids (66.05 kDa)) activate phosphoinositide-specific phospholipase C; M_2 (database code, human, ACM2_HUMAN, 466 amino acids (51.65 kDa)) and M_4 (database code, human, ACM4_HUMAN, 479 amino acids (53.00 kDa)) are negatively coupled to adenylate cyclase; M_2 also increases potassium channel conductance through the action of G-proteins.

Nicotinic acetylcholine receptors are glycosylated multisubunit pentamers with an intrinsic cation-permeable channel with little selectivity among cations; subunit variants include α, β, γ, δ, and ε. After binding acetylcholine, this type of receptor responds by an extensive change in conformation that affects all subunits and leads to opening of an ion-conducting channel across the plasma membrane. *Torpedo* electric organ and embryonic muscle pentamers have $\alpha_2\beta\gamma\delta$, adult mammalian muscle $\alpha_2\beta\delta\varepsilon$, and mammalian neurons $\alpha_2\beta_3$ stoichiometry; subunits are of the four-transmembrane-helix class (the segments being termed M_1 to M_4); bungarotoxin is a selective antagonist. Examples (precursors) from mouse: α, database code ACHA_MOUSE, 457 amino acids (51.88 kDa); β, database code ACHB_MOUSE, 501 amino acids (56.87 kDa); γ, database code ACHG_MOUSE, 519 amino acids (58.68 kDa); δ, database code ACHD_MOUSE, 520 amino acids (59.08 kDa). The neuronal receptor has two subunits (α and non-α); example, precursors α-3 and β-2 (non-alpha) respectively from human: database code ACH3_HUMAN, 502 amino acids (57.05 kDa); and database code ACHN_HUMAN, 502 amino acids (56.95 kDa).

cholinomimetic describing a drug with an acetylcholine-like action.

cholyl the acyl group derived from **cholic acid**.

chondrioma *or* **chondriome** **1** the entire mitochondrial content of a cell. **2** all the hereditary determinants that are localized in mitochondria.

chondriosome *a former name for* **mitochondrion**.

chondroblast a cell that secretes the matrix of **cartilage**.

chondrocalcin the C-terminal peptide formed from amino acids 1173–1418 of human procollagen α_1. Database code (of procollagen α_1) CA12_HUMAN, 1418 amino acids (134.34 kDa).

chondroclast a large, multinucleate cell that digests the cartilage matrix.

chondrocyte a cartilage cell, formed from a **chondroblast**.

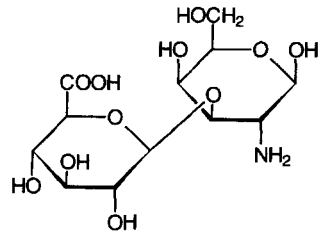
chondroitinase *see* ***N*-acetylgalactosamine-4-sulfatase**, ***N*-acetylgalactosamine-6-sulfatase**.

chondroitinsulfatase *see* ***N*-acetylgalactosamine-4-sulfatase**, ***N*-acetylgalactosamine-6-sulfatase**, **iduronate-2-sulfatase**.

chondroitin sulfate any member of a group of 10–60 kDa glycosaminoglycans, widely distributed in cartilage and other mammalian connective tissues, the repeat units of which consist of β(1–4)-linked D-glucuronylβ(1–3)*N*-acetyl-D-galactosamine sulfate. They usually occur linked to a protein to form proteoglycans. Two subgroups exist, one in which the sulfate is on the 4-position (chondroitin sulfate A) and the second in which it is in the 6-position (chondroitin sulfate C). They often are polydisperse and often differ in the degree of sulfation from tissue to tissue. The chains of repeating disaccharide are covalently linked to the side chains of serine residues in the polypeptide backbone of a protein by a glycosidic attachment through the trisaccharide unit galactosyl–galactosyl–xylosyl. Chondroitin sulfate B is more usually known as **dermatan sulfate**.

chondrosamine *former name for* the D-enantiomer of **galactosamine**, reflecting its presence in **chondrosine**.

chondrosine the disaccharide 2-amino-2-deoxy-3-*O*-β-D-glucopyranuronosyl-D-galactopyranose; *condensed form*: GlcpA(β1-3)GalN. In sulfated form it is the core unit of **chondroitin sulfate**.



chopper **1** a device for chopping tissue e.g. the McIlwain chopper. **2** *(in optics)* a device for interrupting a light beam in a regular manner. For example, in a spectrophotometer it consists of a rotating wheel with alternate silvered and cut-out sectors that is placed in the light beam to allow the light to pass alternately through the sample and the reference cells, the photocell thereby generating an alternating current.

choriocarcinoma a malignant tumour, typically occurring in the uterus, originating as a proliferation of chorionic villi. It may follow pregnancy or develop from a hydatidiform mole. **Choriogonadotropin** is an excellent marker for the presence of this tumour.

choriogonadotropin *or* **chorionic gonadotropin** *or* **choriogonadotrophin** *abbr.*: CG; *the recommended name for* a placental **glycoprotein hormone** that has the gonadotropic activities of both luteinizing hormone (LH) and follicle-stimulating hormone (FSH). It is a member of the family of glycoprotein hormones that includes LH and FSH, the β subunit being specific to choriogonadotropin. It is produced by the corpus luteum after fertilization of the ovum; the blood level rises to a detectable concentration 7–9 days after conception and CG may be detected in urine 1–2 days later, which yields a highly sensitive and specific test for pregnancy. Its administration to males causes increased secretion of testosterone; the lack of such a response indicates testicular failure. It is also a good marker for **choriocarcinoma**. It is a heterodimer of an α chain (identical with that of LH and FSH) and a β chain that confers specificity. Example from *Equus asinus* β chain (precursor): database code LHSB_EQUAS, 169 amino acids (17.94 kDa).

choriomammotropin *or* **chorionic mammotropin** *or* **choriomammotrophin** *abbr.*: CS; *the recommended name for* a placental hormone similar in action to **somatotropin** and **prolactin** and of similar amino-acid sequence to pituitary gonadotropin. It is also known as **chorionic somatomammotropin** or **placental lactogen** (*abbr.*: PL). Example, human lactogen (precursor): database code PLC_HUMAN, 217 amino acids (25.02 kDa).

chorion **1** the highly vascular outermost embryonic membrane of higher vertebrates. In placental animals it has a villous part

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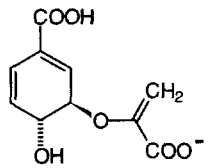
that enters the placenta. **2** membrane of an animal egg, especially the hardened external membrane of an insect's egg.

chorionic gonadotropin *or* **chorionic gonadotrophin** *an alternative name for* **choriogonadotropin**.

chorionic somatomammotropin *or* **chorionic somatomammotrophin** *an alternative name for* **choriomammotropin**.

chorion villus sampling *abbr.*: CVS; a technique for a biopsy of the chorion frondosum during pregnancy to obtain fetal tissue for prenatal diagnosis.

chorismate the anion of (3*R*-*trans*)-3-[(1-carboxyethenyl)oxy]-4-hydroxy-1,5-cyclohexadiene-1-carboxylic acid; the unsymmetrical ether derived from phospho*enol*pyruvate and 5-phosphoshikimic acid (*see* **shikimate pathway**); it is formed as an intermediate in the biosynthesis of aromatic amino acids and many other compounds. The common pathway to aromatic amino acids bifurcates at chorismate: one branch, the prephenate pathway, leads to phenylalanine and tyrosine; the other branch, the anthranilate pathway, leads to tryptophan. There are many other branchpoints in the shikimate pathway. (Note: the configurations can be stated as 3*R*,4*R*.)



chorismate mutase EC 5.4.99.5; an enzyme that catalyses the conversion of chorismate to prephenate. It is the first enzyme in the branch of the **shikimate pathway** that leads to synthesis of phenylalanine. Isoenzymes are found in cytoplasm and in chloroplasts. The chloroplast isoenzyme is activated by tryptophan and inhibited by phenylalanine and tyrosine. Example from yeast: database code CHMU_YEAST, 256 amino acids (29.71 kDa). For an example see **prephenate dehydratase**.

chorismate synthase EC 4.6.1.4; *other name*: 5-*enol*pyruvylshikimate-3-phosphate phospholyase; an enzyme that catalyses the formation of chorismate from 5-*O*-(1-carboxyvinyl)-3-phosphoshikimate with release of orthophosphate. Example from *Escherichia coli*: database code AROC_ECOLI, 360 amino acids (38.96 kDa). *See also* **shikimate pathway**.

Christmas disease *or* **hemophilia B** a sex-linked inherited disorder of **blood coagulation** due to a deficiency of coagulation factor IX (Christmas factor) activity in the blood. It occurs in humans, dogs, cats, and other species, but is less common than classical **hemophilia** (hemophilia A) from which it can only be differentiated by laboratory tests.[After S Christmas, the first described sufferer of the disease.]

Christmas factor *an alternative name for* **factor IX**. *See also* **blood coagulation**, **Christmas disease**.

chrom+ *see* **chromo+**.

chromaffin *or* **chromaffine** describing a tissue, cell, or subcellular granule that stains deeply with chromium salts.

chromaffin tissue a tissue made up of modified neural cells (chromaffin cells) that synthesize, store, and secrete catecholamines. The catecholamines are stored in special subcellular organelles, **chromaffin granules**, ready for release. Chromaffin tissue is found in all vertebrates, at various bodily locations but especially in the medulla of the adrenal gland.

chromat+ *see* **chromato+**.

chromatic of, or related to, colour.

chromatid one of the two daughter strands of a duplicated chromosome that become apparent between early prophase and metaphase in mitosis and between diplotene and second metaphase in meiosis.

chromatin the network of fibres of DNA and protein that make up the **chromosomes** of the eukaryotic nucleus during interphase. It stains strongly with basic dyes. Some parts of the chromosomes are highly dispersed (called **euchromatin**) and other parts are highly condensed (called **heterochromatin**). Chromatin is made up of repeating units, each unit consisting of some 200 DNA base pairs and two each of **histones** H2A, H2B, H3, and H4; most of the DNA is wound around the outside of a core of histones to form **nucleosomes**. The remainder of the DNA, linker DNA, joins adjacent nucleosomes, thereby contributing flexibility to the **chromatin fibre**, a flexibly jointed chain of nucleosomes.

chromatin body a body, containing ribosomal DNA, that occurs during early oogenesis in some water beetles. It disappears at about the time of vitellogenesis and its contents become dispersed in the nuclear interior.

chromatin fingerprinting a two-dimensional electrophoretic technique for simultaneously mapping the total distributions of DNA sizes, protein compositions, and nuclease-mediated precursor–product relationships present in heterogeneous populations of mono- and polynucleosomes. Chromatin, partially digested with micrococcal nuclease, is electrophoretically separated in the first dimension in the presence of inactive DNase I. Subsequently the enzyme is activated by incubating the gel in a magnesium ion-containing buffer and the histones are then separated by electrophoresis in the second dimension.

chromato+ *or (before a vowel)* **chromat+** *comb. form* **1** denoting colour or coloured. **2** denoting **chromatin**. **3** indicating **chromatogram**, **chromatograph**, or **chromatography**.

chromatofocusing a column-chromatographic technique of high capacity and high selectivity for separating proteins according to their isoelectric points. A pH gradient is formed in a column containing an anion exchanger, by use of a special eluting buffer containing a large number of differently charged species. Proteins emerge from the column as a series of sharply focused zones in descending order of their p*I* values, with peak widths in the range 0.04–0.05 pH unit.

chromatogram the result of a chromatographic separation. It may be directly visible, e.g. in the form of a column or strip of material, or, after processing of data, take the form of a graph.

chromatograph **1** to effect a separation by **chromatography**. **2** an apparatus with which to carry out a particular form of chromatography. —**chromatographic** *adj.*; **chromatographically** *adv.*

chromatography any technique, analytical or preparative, for separating the components of a mixture by differential adsorption of compounds to adsorbents, partition between stationary and mobile immiscible phases, ion exchange, or a combination of these. *See* individual entries for the many different types of chromatography; these include: adsorption, affinity, affinity-elution, ampholyte-displacement, argentation, ascending, biospecific-elution, charge-transfer, chromatography, circular, countercurrent, covalent, descending, dye-ligand, electro, exclusion, frontal, gas, gas–liquid, gel-filtration, gel-permeation, high-performance liquid-affinity, high-performance liquid, high-pressure liquid, hydrophobic, ion-exchange, ion-exclusion, ionic-interaction, ion-moderated partition, ligand-mediated, liquid, liquid–liquid, metal-chelate affinity, molecular-exclusion, molecular-sieve, negative, paper, partition, permeation, positive, pseudo-affinity, reverse(d)-phase, salting-out, sievorptive, steric-exclusion, subunit-exchange, thermal-elution, thin-layer, triazine-dye affinity.

chromatophore **1** a pigment-containing cell, especially one in the integument of an animal, that is capable of changing the apparent skin colour by contracting or expanding. **2** any of the particles isolated from photosynthetic organisms that contain photosynthetic pigments, e.g. a **chromoplast**, or membrane fragments from photosynthetic bacteria.

chromatopile a stack of filter papers, of the same diameter, that is compressed in a chromatographic column in large-scale separations.

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chromatoplate the plate that is covered with the support during **thin-layer chromatography**.

chromatosome a **nucleosome** lacking the linker DNA.

+chrome *comb. form* denoting colour, coloured, or pigment.

chromium *symbol*: Cr; the element of proton number 24. It is a paramagnetic, metallic transition element of group 6 of the IUPAC **periodic table**, with oxidation states of II, III, and IV. Natural chromium has a relative atomic mass of 51.966 and is a mixture of four stable nuclides with nucleon numbers of 50, 52, 53, and 54, the predominant one being chromium-52 (relative abundance 83.789 atom percent). A number of artificial radioactive nuclides are known, of which **chromium-51** is the longest lived. Chromium has an abundance of about 0.02% of the igneous rocks of the earth and it occurs in nature exclusively in the combined form, the mixed oxide chromite $Fe_2Cr_2O_4$ being the chief ore. It is an essential dietary trace metal, but functions in the body primarily as a component of **glucose-tolerance factor**, the chief symptom of experimental chromium deficiency in animals being impaired glucose tolerance.

chromium-51 the artificial radioactive nuclide of chromium, $^{51}_{24}Cr$. It decays by electron capture, 9.8% of nuclei emitting γ-radiation (0.32 MeV); it also emits X-rays (0.005 MeV, 22%) but no β-particles; it has a half-life of 27.7 days. It is used as chromate for labelling blood cells, and as the 1:1 complex of Cr^{2+} with EDTA for measuring glomerular filtration rate.

chromo+ *or (before a vowel)* **chrom+** *comb. form* **1** denoting colour, coloured, or pigment. **2** indicating **chromium**.

chromobindin *see* **annexin I**, **annexin II**, **annexin IV**, **annexin VI**.

chromogen **1** the colourless precursor of a dye or pigment, that is converted into the dye or pigment, e.g. by oxidation. **2** a compound containing a **chromophore** that is not itself coloured but becomes so when an auxochromic group (*see* **auxochrome**) is introduced into the molecule. **3** any microorganism that produces pigment.

chromogenic **1** producing colour. **2** of, or pertaining to, a **chromogen**.

chromogenic substrate a substrate that, when acted on by an enzyme, gives rise to a coloured product.

chromogranin *abbr.*: Cg; either of two soluble proteins, originally discovered in bovine chromaffin granules (*see* **chromaffin tissue**) but now known to be widely distributed in endocrine (including neuroendocrine) tissues. They are designated chromogranin A (CgA) and chromogranin B (CgB; *also called* **secretogranin I**). Both proteins are acidic (pI 4.5–5.0), but homology is limited except in the N-terminal and C-terminal regions, and there is a lack of immunological reactivity. Both have been detected immunologically in various mammals, amphibians, birds, and fishes; CgA also occurs in *Drosophila*. CgA is a 430 amino acid Ca^{2+}-binding glycoprotein; it is hydrophilic with no hydrophobic stretches, and is co-secreted with many hormones from, e.g., pancreas and thyroid C cells. Both proteins have **dibasic cleavage sites** for endopeptidases, the action of which leads to the formation of several active peptides: CgA yields **parastatin** (porcine $CgA_{347–419}$), an inhibitor of low calcium-stimulated parathyroid cell secretion; **pancreastatin** (porcine $CgA_{240–288}$), an inhibitor of glucose-induced insulin release from the pancreas; **chromostatin** (bovine $CgA_{124–143}$), an inhibitor of catecholamine release by chromaffin cells; **vasostatin** (bovine $CgA_{1–76}$); **beta-granin** (bovine $CgA_{1–114}$), an inhibitor of parahormone secretion; and a peptide WE-14. CgB is co-secreted from adrenal medulla with catecholamines, from sympathetic nerve with norepinephrine, and from some cell lines; proteolytic cleavage releases several peptides of unknown function. Example (incomplete but contains entire CgA sequence) from pig: database code CMGA_PIG, 446 amino acids (48.83 kDa).

chromomere any of the beadlike concentrations of **chromatin** that are arranged linearly along a **chromosome**.

chromonema (*pl.* **chromonemata**) *cytological term for* **1** all of the threads which make up the **nuclear reticulum**. **2** any of the smallest strands of DNA in a chromosome or chromatid. **3** a twisted chromatid thread within the chromosome.

chromophore any functional grouping within a molecular entity that gives rise to the colour (or characteristic absorption spectrum) of the substance.

chromoplast any coloured **plastid** containing carotenoid pigments but not chlorophyll. Chromoplasts give the yellow to red colours of many flowers (e.g. daffodil), fruits (e.g. tomato), and some roots (e.g. carrot).

chromoprotein any of a class of proteins that contain a colour-producing group or **chromophore**. Both chlorophylls and carotenoids exist in chloroplasts as chromoproteins.

chromosome a structure composed of a very long molecule of **DNA** and associated proteins (e.g. **histones**) that carries hereditary information. Chromosomes are especially evident in plant or animal cells undergoing mitosis or meiosis, where each chromosome becomes condensed into a compact, readily visible thread. In nondividing cells chromosomes typically assume a more dispersed form called **chromatin**. The number of chromosomes is characteristic for the species concerned. In a bacterium only one chromosome is evident as the cell is about to divide. After DNA replication, the two new chromosomes attach to a specialized site on the bacterial plasma membrane for segregation to the two daughter cells. —**chromosomal** *adj.*

chromosome mutation a type of **mutation** (def. 1) involving alteration(s) in chromosome structure.

chromosome walking a method used to identify which clone in a gene bank contains a desired gene or sequence that cannot easily be selected for. The gene bank must contain the entire DNA sequence of the chromosome as a series of overlapping fragments. A series of **colony hybridizations** is carried out, starting with a cloned gene that has already been identified and that is known to be on the same chromosome as the desired gene. This identified gene is used as a probe to pick out clones containing adjacent sequences. These are then used in turn as probes to identify clones carrying sequences adjacent to them, and so on. At each round of hybridization one 'walks' further along the chromosome from the identified gene.

chromostatin a 20-amino-acid peptide that can be released *in vitro* by the proteolytic cleavage of **chromogranin A**. It potently inhibits catecholamine release by **chromaffin** cells induced by carbamoylcholine or by depolarizing K^+ concentration, and it inhibits secretagogue-induced calcium influx. Its physiological status is uncertain – it is not flanked by **dibasic cleavage sites** in the precursor.

chronic **1** continuing over a long time; repeatedly recurring. **2** *(of a disease)* developing slowly or lasting for a long time.

chrono+ *or (before a vowel)* **chron+** *comb. form* denoting time.

chronobiochemistry the branch of biochemistry concerned with the biochemical aspects of **chronobiology**, the study of the inherent rhythmicity or periodicity of living organisms and their activities.

chrysolamarin *see* **callose**.

chrysotherapy the use of gold-containing substances in the treatment of disease.

CHS *(in clinical biochemistry) abbr. for* cholinesterase (def. 1).

ChTX *abbr. for* charybdotoxin.

chyle the white lymph found in the lymph vessels of the intestine (lacteals) during the digestion of fats. It contains globules with a high fat content. *See also* **chylomicron**.

chylomicron a large lipoprotein particle, of molecular mass up to 10^7 kDa, measuring up to 100 nm in diameter, and of density < 1.006. The approximate composition (% by weight) of chylomicrons is 2% cholesterol, unesterified; 5% cholesterol, esterified; 7% phospholipid; 84% triacylglycerol; 2% protein. Their apolipoprotein composition (% by weight total apolipoprotein) is 7.4% A-I; 4.2% A-II; 22.5% B-48; 66% C-I + C-II + C-III. Chylomicrons are formed in the mucosa of the small intestine, and contain mostly triacylglycerols re-esterified in the mucosal cells from dietary long-chain fatty acids associated with apolipoproteins. They then enter the lymphatic

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capillaries (lacteals) of the intestinal villi, and thence the bloodstream. They are the vehicle by which fat is absorbed into the body.

chymase EC 3.4.21.39; *other names*: mast cell protease I; skeletal muscle (SK) protease. An enzyme that catalyses preferential cleavage of the bonds: Phe-|-Xaa > Tyr-|-Xaa > Trp-|-Xaa > Leu-|-Xaa. It is a trypsin-like serine proteinase, and a homologue of chymotrypsin; it is found in mast cell granules (heart, lung, etc.). Example, human (precursor): database code MCP1_HUMAN, 247 amino acids (27.29 kDa).

chyme the semifluid mass of partially digested food that passes through the pylorus of the stomach into the small intestine.

chymopapain EC 3.4.22.6; *other name*: papaya proteinase II; the major endopeptidase enzyme of papaya (*Carica papaya*) latex; its specificity is similar to that of **papain**. The protein from that species is: database code PAP2_CARPA, 218 amino acids (23.66 kDa).

chymosin *or* **rennin** EC 3.4.23.4; an aspartic proteinase enzyme that cleaves a single bond in κ **casein** (Ser-Phe^{105}-|-Met-Ala) and is responsible for clotting of milk. It is produced from a precursor in the mucosa of the fourth stomach of calves. It is now produced by cDNA technology. Example (bovine): database code NRL_1CMS, 323 amino acids (35.61 kDa); 3-D structure is known. (*Note*: use of the synonym rennin is now deprecated because of possible confusion with **renin**.)

chymotrypsin a serine endopeptidase, EC 3.4.21.1, formed from the proenzyme **chymotrypsinogen** by the action of trypsin. In vertebrates, chymotrypsins are contained in **pancreatic juice**, and hydrolyse protein in the small intestine. Chymotrypsinogen is synthesized in the acinar cells of the exocrine pancreas and stored in **zymogen granules** until released. Several forms of chymotrypsin are found: **Chymotrypsin A** is formed from bovine and porcine chymotrypsinogen A. It will hydrolyse peptides, amides, and esters, preferentially at the carbonyl end of Tyr, Trp, Phe, and Leu residues. **Chymotrypsin B**, formed from chymotrypsinogen B, is homologous with chymotrypsin A. **Chymotrypsin C**, EC 3.4.21.2, is formed from porcine chymotrypsinogen C and from bovine subunit II of procarboxypeptidase A. It preferentially cleaves at the carbonyl end of Leu, Tyr, Phe, Met, Trp, Gln, and Asn residues. Enzymes homologous to and with similar specificities to chymotrypsin have been isolated from many species. Chymotrypsinogens are synthesized as a single 245-residue polypeptide chain cross-linked by five disulfide bonds. This is fully activated when the bond between Arg^{15} and Ile^{16} is cleaved by trypsin to yield π-chymotrypsin; subsequent autocatalytic cleavage of more peptide bonds (to remove 14–15, 147–148) converts it into α-chymotrypsin. Amino acids 1–13 form chymotrypsin A-chain, 16–146 form chymotrypsin B-chain, and 149–245 form chymotrypsin C-chain, the three chains being covalently linked by disulfide bonds, 1–122, 42–58, 136–201, 168–182, and 191–220. The mechanism involves a **charge-relay system** of His^{57}, Asp^{102}, and Ser^{195}. Chymotrypsin is more active than trypsin against certain esters, e.g. *N*-acetyl-L-tyrosine ethyl ester. Chymotrypsin binds α_1-antitrypsin. Example (bovine): database code CTRA_BOVIN, 245 amino acids (25.64 kDa). 3-D structure known.

chymotrypsinogen *see* **chymotrypsin**.

chymotryptic of, or relating to, **chymotrypsin**; **chymotryptic digestion** is the partial hydrolysis of a protein by chymotrypsin.

Ci *symbol for* curie.

cI *or* **cI** *symbol for* lambda repressor.

CI *abbr. for* Colour Index (especially as a prefix to the identifying number for a particular dye or stain).

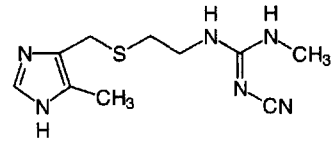
CIDNP *abbr. for* chemically induced dynamic nuclear polarization.

CIE *abbr. for* counterimmunoelectrophoresis.

ciliatine *see* **phosphono+**.

cilium (*pl.* **cilia**) a specialized eukaryotic locomotor organelle that consists of a filiform extrusion of the cell surface. Each cilium is bounded by an extrusion of the cytoplasmic membrane, and contains a regular longitudinal array of **microtubules**, anchored basally in a **centriole**. *Compare* **flagellum**. — **ciliary** *adj.*

cimetidine *N*-cyano-*N'*-methyl-*N''*-[-2-[[(5-methyl-1*H*-imidazol-4-yl)methyl]thio]ethyl]guanidine; a competitive antagonist of histamine H_2 receptors used clinically as an anti-ulcer drug; it inhibits gastric acid secretion and reduces the output of pepsin. One proprietary name is Tagamet.



cIMP *abbr. for* cyclic IMP; *see* **inosine 3',5'-phosphate**.

cin4 the gene for the enzyme ***trans*-cinnamate 4-monooxygenase** found in many plants.

cinchonine an alkaloid obtained from cinchona bark and possessing antimalarial properties. *See also* **quinine**.

cinnamate the anion of 3-phenyl-2-propenoic acid; *trans*-cinnamate (3-phenyl-2*E*-propenoate) is a compound formed from phenylalanine by phenylalanine ammonia-lyase, EC 4.3.1.5; it is the precursor of ferulic and sinapic acids in the pathway for **lignin** synthesis.

***trans*-cinnamate 4-monooxygenase** *abbr.*: CA4H; EC 1.14.13.11; *systematic name*: *trans*-cinnamate,NADPH:oxygen oxidoreductase (4-hydroxylating); *other names*: cinnamic acid 4-hydroxylase; cinnamate 4-hydroxylase. An enzyme that catalyses a reaction between *trans*-cinnamate, NADPH, and dioxygen to form 4-hydroxycinnamate, $NADP^+$, and H_2O. It is an endoplasmic reticulum enzyme of high specificity – it does not act on amino acids, phenylacetate, or benzoate – and is the first enzyme in the pathway from **cinnamate** to **lignin**. Example from *Catharanthus roseus*: database code CRCIN4HX, 505 amino acids (58.21 kDa).

cinoxacin azolinic acid; 1-ethyl-1,4-dihydro-4-oxo[1,3]dioxolo[4,5-*g*]cinnoline-3-carboxylic acid; a **4-quinolone antibiotic** with activity against Gram-negative bacteria through the inhibition of DNA gyrase.

ciprofloxacin a fluorinated **4-quinolone antibiotic** active against both Gram-positive and Gram-negative bacteria although more so against the latter and also active against *Chlamydia* and mycobacteria.

circadian describing biological activity (e.g. behavioural, physiological, metabolic) that exhibits an endogenous periodicity of approximately 24 hours independently of any daily variation in the environment. *Compare* **diurnal**, **infradian**, **ultradian**. [From Latin *circa*, about, + *dies*, day.]

Circe effect the phenomenon underlying any physicochemical description of the action of an enzyme upon a substrate. It refers to the strong attractive forces that bind the substrate into the active site of the enzyme, where it undergoes a radical transformation of form and structure. It is named after the sorceress, Circe, who according to Greek mythology transformed the men of Odysseus into beasts.

circular birefringence the **birefringence** produced by left and right circularly polarized light.

circular chromatography a technique of paper chromatography in which the substances to be separated are allowed to travel radially from the centre of a filter-paper disk. The material is applied to the centre of the disk from which a small sector is cut out and folded down to allow it to dip into the eluting solvent.

circular chromosome a circular DNA duplex, the form taken by the chromosomes of some prokaryotic organisms, e.g. *Escherichia coli*, *Bacillus subtilis*, and *Pseudomonas aeruginosa*.

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circular dichroism *abbr.*: CD; the difference in absorption of left and right circularly polarized light. The shape and magnitude of the CD curve as a function of wavelength of solutions of proteins (and other macromolecules) are sensitive to changes in conformation of these solutes. *See also* **Cotton effect**, **ellipticity**, **molecular ellipticity**, **optical rotatory dispersion**.

circular DNA any single- or double-stranded DNA molecule with a circular (but not necessarily geometrically circular) structure. If single-stranded, the circle is closed covalently, but if double-stranded, one or both strands may be open. *See also* **covalent (closed) circle of DNA**.

circularly polarized light *see* **polarized light**.

cis *abbr.*: c; *conformational descriptor* denoting synperiplanar (use not recommended); *see* **conformation**.

cis- *abbr.*: c-; *prefix (in chemical nomenclature)* denoting that two specified substituents lie on the same side of a reference plane in the molecule. (*cis* means 'on this side'.) In systematic names it is denoted by the symbol *Z*. *See* ***cis–trans* isomerism**, ***E/Z* convention**. *Compare* ***trans-***.

***cis*-acting** *(in genetics)* describing a regulatory genetic element whose effects are sensitive to its position relative to the gene being regulated, i.e. on the same molecule of DNA. Examples include bacterial **operators**.

***cis* configuration** *(in genetics)* describing the configuration of two linked heterozygous genes in which both wild-type alleles occur on one of the paired homologous chromosomes while the mutant alleles occur on the other homologue; i.e. (++/*ab*). *Compare* ***trans* configuration**.

***cis* isomer** *see* ***cis–trans* isomer**.

CISP *abbr. for* corticotropin-induced secreted protein; now called thrombospondin-2 (*see* **thrombospondin**).

cisplatin *cis*-diammineplatinum(II) dichloride; *cis*-diaminedichloroplatinum; a substance that interacts with, and forms cross-links between, DNA and proteins. It is used as a neoplasm inhibitor to treat solid tumours, primarily of the testis and ovary.

cisterna (*pl.* **cisternae**) **1** *(in cytology)* the flattened, saclike space enclosed between paired membranes of the **endoplasmic reticulum** and the **Golgi apparatus**. **2** *(in anatomy)* an enlarged space, such as the cisterna magna in the rear of the brain or the cisterna chyli between the crura of the diaphragm. —**cisternal** *adj.*

***cis–trans* complementation test** a genetic test to determine whether two gene mutations (*a* and *b*) occur in the same functional gene (or **cistron**). It involves comparison of heterozygotes in which the relevant mutations are in the same chromosome, i.e. in the *cis* configuration (++/*ab*), with heterozygotes in which the mutations are in separate chromosomes, i.e. the *trans* configuration (*a*+/+*b*).

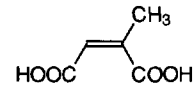
cis–trans* isomer** *or (sometimes)* **geometric isomer** *or* **geometrical isomer** either of a pair of **diastereoisomers** that differ only in the positions of atoms relative to a specified reference plane in the molecules, in cases where these atoms are, or are considered as if they were, parts of a rigid structure. The two isomers are designated the *cis* isomer and the *trans* isomer when the two particular atomic groupings lie respectively on the same or on opposite sides of the reference plane. *See also* ***cis–trans* isomerism**. —cis–trans*-isomeric** *adj.*

***cis–trans* isomerism** *or (sometimes)* **geometrical isomerism** the phenomenon of the existence of *cis–trans* isomers in general, or the occurrence of paired *cis* and *trans* isomers in a particular molecule. Atoms or groups are termed *cis* or *trans* to one another when they lie respectively on the same or on opposite sides of a reference plane identifiable as common among stereoisomers. For compounds containing only doubly bonded atoms the reference plane contains the double-bonded atoms and is perpendicular to the plane containing these atoms and those directly attached to them. For cyclic compounds the reference plane is that in which the ring skeleton lies or to which it approximates. *See also* ***E/Z* convention**.

cistron a unit of DNA sequence that codes for a single polypeptide or protein. It may be a smaller unit than the **gene**, which contains the unit of DNA determining a single character. Whether or not a cistron is the same as a gene can be determined by the ***cis–trans* complementation test**, hence the name cistron (*cis* means 'on this side').

Cit *symbol for* a residue of the α-amino acid L-citrulline.

citraconate **1** *the trivial name for* methylmaleate, *cis*-1,2-propylenedicarboxylate, (*Z*)-2-methyl-2-butenedioate, the dianion of citraconic acid, (*Z*)-2-methyl-2-butenedioic acid. **2** any mixture of citraconic acid and its mono- and dianions. **3** any salt or ester of citraconic acid.



citraconic acid

citraconoyl the bivalent *cis*-acyl group, –CO–CH=C(CH_3)–CO–, derived from citraconic acid. *Compare* **citraconyl**.

citraconyl either of the isomeric univalent *cis*-acyl groups, HOOC–C(CH_3)=CH–CO– or HOOC–CH=C(CH_3)–CO–, derived from citraconic acid. *See also* **citraconylation**.

citraconylation introduction of one or more **citraconyl** groups into a substance by acylation. Similarly to **maleylation** (and succinylation), citraconylation of a protein with citraconic anhydride is used to acylate its free lysine (and other) amino groups in order to change their charge at neutral pH from positive to negative and to render the adjacent peptide bond resistant to hydrolysis by trypsin. Reaction occurs at pH 8 and the citraconyl groups can be removed at pH 3.5 (both operations at 20°C). Introduction of citraconyl groups is slower than is the case with maleyl groups, but their removal is faster and more complete. —**citraconylate** *vb.*; **citraconylated** *adj.*

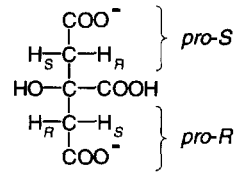
citrase *see* **citrate lyase**.

citratase *see* **citrate lyase**.

citrate **1** *the trivial name for* β-hydroxytricarballylate, 2-hydroxy-1,2,3-propanetricarboxylate,

$$HO–C(CH_2–COO^-)_2–COO^-,$$

the trianion of citric acid, 2-hydroxy-1,2,3-propanetricarboxylic acid. **2** any mixture of free citric acid and its anions; the trianion is the predominant form at physiological pH values. It is widely distributed in nature and is an important intermediate in the **tricarboxylic-acid cycle** and the **glyoxylate cycle**. Citrate (alone or in mixtures) is useful as a buffer; pK_{a1} (25 °C) = 3.13, pK_{a2} (25 °C) = 4.76, pK_{a3} (25 °C) = 6.40. It is useful also as a component of anticoagulant solutions and has many commercial applications in the chemical, food, pharmaceutical, and other industries. Industrial production of citrate is usually by fermentation of inexpensive sources of glucose or sucrose with selected strains of *Aspergillus niger*; world production in 1992 was 5×10^8 tons. **3** any (partial or full) salt or ester of citric acid.



citrate aldolase *see* **citrate lyase**.

citrate cleavage enzyme EC 4.1.3.8; *recommended name*:

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ATP–citrate (*pro-S*)-lyase. An enzyme that catalyses a reaction between ATP, citrate, and CoA to form acetyl-CoA, oxaloacetate, ADP and orthophosphate. In mammals it participates in the release of acetyl-CoA in the cytosol, particularly as a precursor for fatty acid synthesis, there being no system for transporting excess acetyl-CoA out of the mitochondrion. The acetyl carbons are thus transported across the mitochondrial membrane as citrate and then released by this enzyme. Example from rat, homotetramer: database code ACLY_RAT, 1100 amino acids (120.50 kDa).

citrate cycle *another name for the* **tricarboxylic-acid cycle**.

citrate (*pro*-3*S*)-lyase EC 4.1.3.6; *other names*: citrase; citratase; citritase; citridesmolase; citrate aldolase; a bacterial enzyme that catalyses the formation of acetate and oxaloacetate from citrate. Example from *Klebsiella pneumoniae*: database code CILB_KLEPN 289 amino acids (31.32 kDa). ATP–citrate lyase is another name for **citrate cleavage enzyme**.

citrate (*Re*)-synthase EC 4.1.3.28; an enzyme from some bacteria that forms citrate with the incoming $-CH_2-COOH$ group in the *pro-R* position of citrate. The addition is to the *Re*-face of the carbonyl group of oxaloacetate.

citrate (*Si*)-synthase EC 4.1.3.7; *other names*: citrogenase; oxaloacetate transacetase; condensing enzyme; citrate condensing enzyme. An enzyme that catalyses a reaction between acetyl-CoA, H_2O, and oxaloacetate to form citrate and CoA. It synthesizes citrate from oxaloacetate and acetyl-CoA, placing the incoming $-CH_2-COOH$ in the *pro-S* position in citrate (*see* **oxaloacetate**). The addition is to the *Si*-face of the carbonyl group of oxaloacetate. This is the usual mammalian citrate synthase; mitochondrial enzymes are closely related homodimers (six motifs). Example from chicken: database code CISY_CHICK, 433 amino acids (46.88 kDa); 3-D structure known.

citric acid *see* **citrate**.

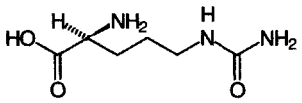
citric-acid cycle *an alternative name for* **tricarboxylic-acid cycle**.

citridesmolase *see* **citrate lyase**.

citritase *see* **citrate lyase**.

citrovorum factor *(formerly) an alternative name for* **folinic acid**.

citrulline N^5-carbamoyl-L-ornithine; 2-amino-5-ureiodovaleric acid; an α-amino acid, not found in proteins. L-Citrulline is an intermediate in the **urea cycle** in animals and in a modified urea cycle in plants. It was first isolated from the juice of watermelon, *Citrullus vulgaris*.



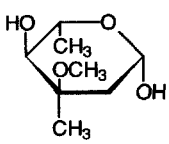
citrullinemia *or* **citrullinuria** an autosomal recessive genetic disease involving a deficiency of the enzyme **argininosuccinate synthase**. It is characterized by a high plasma citrulline level and excessive secretion of the amino acid in the urine. It results in neurological damage and mental retardation.

CJD *abbr. for* Creutzfeldt–Jakob disease.

C-kinase *see* **protein kinase C**.

Cl *symbol for* chlorine.

cladinose 2,6-dideoxy-3-*C*-methyl-3-*O*-methyl-L-*ribo*-hexose; 3-*O*-methyl mycarose; a component of **erythromycins** A and B.



β-L anomer

cladistics a method of classification that attempts to reconstruct a **phylogeny** using characters that are unique to each taxonomic group. The term **cladistic** is currently used to describe an evolutionary or phylogenetic tree based on gene sequence similarities and gene association.

cladogenesis a process of adaptive evolution leading to the development of a greater variety of organisms; branching evolution. —**cladogenetic** *adj.*

cladogram a diagram depicting **cladogenetic evolution**, i.e. the evolution of some character through the descendants of a common ancestor.

clarify to make or become clear, especially to remove finely divided suspended material from a solution, e.g. by centrifugation or filtration. —**clarified** *adj.*; **clarification** *n.*

Clark and Lubs buffers one of the early series of buffer mixtures of predetermined pH, covering the range pH 2.2–10.0. [After William Mansfield Clark (1884–1964), US biochemist, and Herbert A. Lubs.]

Clark electrode a type of **oxygen electrode**. [After Leland Charles Clark (1918–).]

class a taxonomic category ranking below the **phylum** (or division) and containing several **orders** (or sometimes only a single order).

classical pathway of complement activation *see* **complement**.

class switch a change (switch) in the expression of B lymphocytes from one class of antibody to another.

clastic dividing into parts, especially of a chemical reaction in which one molecular species is divided into parts; e.g. phosphoroclastic, thioclastic.

clastogen an agent that is able to bring about breakage in chromosomes. —**clastogenic** *adj.*

clathrate **1** *or* **cage compound** *(in chemistry)* a solid complex or an addition compound in which the crystal lattice or structure of one component (the **host molecule**) completely encloses spaces in which a second component (the **guest molecule**) is located. There is no chemical bonding between the two components. *Compare* **inclusion complex**. **2** designating or relating to a clathrate. **3** *(in biology)* lattice-shaped.

clathrin a 180 kDa protein that is the main component of the coat of **coated vesicles** and **coated pits**, which are concerned in the transfer of molecules between the membranous components of eukaryotic cells. Clathrin also occurs in **synaptic vesicles**. The clathrin coat is a polyhedral lattice of subunits; each subunit, or clathrin **triskelion**, comprises three heavy chains and three light chains. Examples from rat; light chain A: database code CLCA_RAT, 248 amino acids (26.95 kDa); light chain B: database code CLCB_RAT, 229 amino acids (25.09 kDa); heavy chain: database code CLH_RAT, 1675 amino acids (191.38 kDa).

clathrin uncoating protein *or* **uncoating ATPase** a protein from brain or erythrocyte cytosol that disassembles **clathrin** coats to **triskelions** in an ATP-dependent manner. Present in substantial excess of clathrin triskelions, it binds to a C-terminal domain of the heavy chain of clathrin triskelions.

Claude, Albert (1899–1983), Belgian-born US cell biologist distinguished for his development of methods of separating cellular components by differential centrifugation and for identifying mitochondria as the primary cellular site for biological oxidation; Nobel Laureate in Physiology or Medicine (1974) jointly with C. R. M. J. de Duve and G. E. Palade 'for their discoveries concerning the structural and functional organization of the cell'.

clavulanic acid 3-(2-hydroxyethylidene)-7-oxo-4-oxa-1-azabicyclo[3.2.0]heptane-2-carboxylic acid; a weak antibacterial agent but potent β-lactamase inhibitor produced by *Streptomyces clavulingerus*. It protects lactamase-sensitive but otherwise potent antibiotics from deactivation, and is used in combination with β-lactam antibiotics to increase their efficacy. It has no antibacterial activity but by inactivating penicillinases it makes a combination active against penicillin-

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resistant bacteria. These include *Staphylococcus aureus*, 50% of many *Bacteroides*, and *Klebsiella* spp. A commonly used proprietary combination is Augmentin.

clearance *(in physiology) symbol*: *C*; a measure of the efficiency of the kidney in removing a substance from the blood. $C = UV/P$, where U and P are the concentrations of the substance in the urine and plasma, respectively, and V is the rate of urine flow in ml min^{-1}. Clearance is therefore a rate, with the dimensions of ml plasma per min.

clearing **1** *(in histology)* the process of preparing tissue samples for microscopical examination by removing the dehydrating agent and rendering the sample transparent. **2** *(in physiology)* the removal of a substance from the body or from the blood; *see* **clearance**.

clearing factor lipase *an alternative name for* **lipoprotein lipase**; an enzyme found in the capillary endothelium of various tissues, notably heart, lung, and adipose tissue, so called because it clears the opalescence from lipemic plasma.

cleavage **1** the tendency of a crystal to split in certain preferred directions with the formation of smooth surfaces, or the act of so splitting a crystal; hence **cleavage plane**, **cleavage face**. **2** the rupture of a (usually specified) chemical bond in a molecule with the formation of smaller molecules. **3** *or* **segmentation** *(in embryology)* the series of mitotic divisions by which a fertilized animal ovum changes, without any overall change in size, into a ball of smaller cells constituting the primitive embryo.

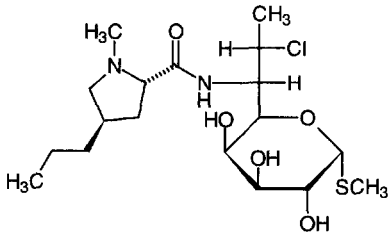
cleavage division the mitotic division of a fertilized egg up to the point at which the regions of the egg shift relative to each other.

cleave to split or cause to divide, especially along the line of a natural weakness; to split a chemical bond; to effect or undergo **cleavage**. —**cleavable** *adj.*

Cleland's reagent *see* **dithiothreitol**. [After William Wallace Cleland (1937–).]

climacteric **1** *(in medicine)* the female menopause, or the corresponding time of life in men. **2** *(in botany)* the marked increase in respiration in fruit just prior to and during ripening.

clindamycin (7*S*)-7-chloro-7-deoxylincomycin; a semisynthetic antibiotic that is useful against anaerobic bacteria; for structure and action *see* **lincomycin**, **lincosamide**.



clinical of, or pertaining to, the course of disease in an individual, or the examination and treatment of an individual directly, as opposed to the laboratory investigation of disease.

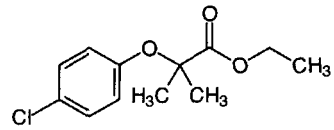
clinical chemistry a branch of applied biochemistry concerned with the nature and determination of chemical substances of interest in the investigation of diseases.

CLIP *abbr. for* **1** corticotropin-like intermediate peptide. **2** Class-II-associated invariant-chain peptide (*see* Class II MHC antigens in **major histocompatibility complex**).

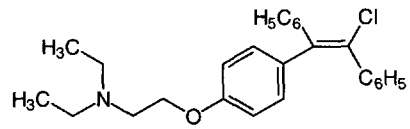
CLIP-170 *see* **restin**.

clofazimine *N*,5-bis(4-chlorophenyl)-3,5-dihydro-3-[(1-methylethyl)imino]-2-phenazinamine; an iminophenazine dye with anti-inflammatory, tuberculostatic, and leprostatic activity. It is used to treat multibacillary or sulfone-resistant leprosy.

clofibrate ethyl 2-(*p*-chlorophenoxy)-2-methylpropionate; 2-(4-chlorophenoxy)-2-methylpropanoic acid ethyl ester; a drug that reduces high plasma levels of triacylglycerols, very-low-density lipoproteins (VLDL), and (less so) cholesterol. Its actions are probably mediated by the stimulation of **lipoprotein lipase**, which reduces the triacylglycerol composition of VLDL and stimulates clearance of low-density lipoproteins by liver. It is used primarily in the treatment of type III (but also in type IV, type V, and type IIb) hyperlipoproteinemia. *Compare* **gemfibrozil**.



clomifene *or* **clomiphene** 2-[4-(2-chloro-1,2-diphenylethenyl)phenoxy]-*N*,*N*-diethylethanamine; an antiestrogenic aminoether derivative of stilbene; it blocks estradiol receptors in the hypothalamus and may stimulate the secretion of gonadotropin-releasing hormone. It is active as an antitumour agent against mammary carcinomas, and can be used to induce ovulation in infertile women. Both its structure and actions are similar to those of **Tamoxifen**.



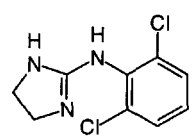
clonal culture any culture of cells produced in such a way that an individual **clone** (def. 1) can be selected.

clonal selection theory *or* **Burnet's theory of immunity** a theory to account for the phenomenon of **acquired immunity** and the ability of the immune system to produce large quantities of highly specific antibody for any particular immunogen. According to the theory, the ability to produce a given antibody is a pre-existing and genetically determined characteristic of a particular clone of B lymphocytes. An encounter with the antigen triggers proliferation of the corresponding clone, producing a greatly expanded population of cells that secrete specific antibody. Some members of the expanded clone assume the role of memory cells, which respond to any subsequent encounter with the same immunogen which accounts for the secondary response being greater than the primary response. *See also* **Burnet**.

clone **1** the descendants produced vegetatively or by apomixis from a single plant, or asexually or parthenogenetically from a single animal; a group of cells produced by division from a single cell. The members of a clone are of the same genetic constitution, unless **mutation** has occurred amongst them. **2** a homogeneous population of DNA molecules; *see* **molecular cloning**. **3** to propagate a selected organism or cell, or to replicate a particular DNA molecule so as to produce a clone. — **clonal** *adj.*; **cloning** *n.*

cloned library *an alternative name for* **gene library**.

clonidine 2,6-dichloro-*N*-2-imidazolidinylidenebenzenamine; an antagonist at α_2 (presynaptic) adrenergic receptors, P_1 purinergic receptors, and H_2 histamine receptors. It is used as a central antihypertensive drug; it also abolishes most symptoms of opiate withdrawal.



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cloning vector *or* **cloning vehicle** the DNA of any transmissible agent (e.g. plasmid or virus) into which a segment of foreign DNA can be spliced in order to introduce the foreign DNA into cells of the agent's normal host and promote its replication and transcription therein. (1) **Plasmid vectors** contain (i) an origin of replication, so that the plasmid can be replicated; (ii) an antibiotic resistance gene to allow selection of transformed host cells; (iii) often, a 'polylinker' containing several different restriction enzyme recognition sites and a second marker gene (e.g. *lacZ*; *see* **X-gal**) which will be inactivated when foreign DNA is inserted therein, thus allowing identification of transformants bearing plasmids containing inserts, rather than 'empty' vectors. Examples include **pBR322** and the **pUC vectors**. *See also* **expression vectors**. (2) **Bacteriophage vectors**, usually based on **lambda phage**, can accommodate longer fragments of foreign DNA. In insertion vectors (e.g. λgt10) the foreign DNA is inserted into the phage DNA while in replacement vectors (e.g. λEMBL4) the foreign DNA is ligated between two phage fragments, or arms. (3) Hybrid vectors, **cosmids**, **phagemids** and **phasmids** (def. 1), with features of both plasmids and phage, have also been constructed. *See also* **molecular cloning**.

closed circle (of DNA) *see* **covalent (closed) circle (of DNA)**.

closed double-stranded DNA *see* **covalent (closed) circle (of DNA)**.

closed duplex DNA *or* **DNA I** a closed double-stranded DNA molecule in which the DNA helical structure is preserved.

closed-loop system a type of system, e.g. a metabolic pathway or an electrical circuit, in which control is exerted by **feedback**. *Compare* **open-loop system**.

closed system any (thermodynamic) system that cannot gain or lose matter, heat, or work. *Compare* **open system**.

close packing the structure of a solid in which nonbonded atoms (or molecules) are surrounded by other nonbonded atoms (or molecules) in such a way that the distance between them is close or equal to the sum of their van der Waals contact radii (*see* **van der Waals radius**).

clostridiopeptidase A the **collagenase** obtained from *Clostridium histolyticum*.

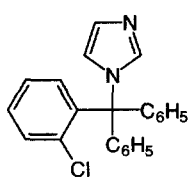
Clostridium a genus of spore-forming rod-shaped bacteria of the family Bacillaceae. Its members are chemoorganotrophic, obligately anaerobic, and typically Gram-positive. They are widespread in soil, mud, and in the intestinal tract of animals. Some species are pathogenic if they gain access to the tissues, and produce a range of toxins.

***Clostridium histolyticum* collagenase** *see* **microbial collagenase**.

clostripain *or* **clostridiopeptidase B** EC 3.4.22.8; a cysteine proteinase enzyme from *Clostridium histolyticum*. It preferentially cleaves Arg-|-Xaa and Arg-|-Pro bonds and is inactivated by substituted arginine and lysine chloromethyl ketones. It is a heterodimer of α and β chains. Example from *C. histolyticum* (α chain): database code CLOS_CLOH1, 526 amino acids (59.73 kDa).

clot retraction the contraction of a blood clot after its formation, accompanied by the expression of serum.

clotrimazole 1-[(2-chlorophenyl)diphenylmethyl]-1*H*-imidazole; an **imidazole** used topically as an antifungal agent. It inhibits ergosterol synthesis and disrupts the transport of amino acids into the fungus.

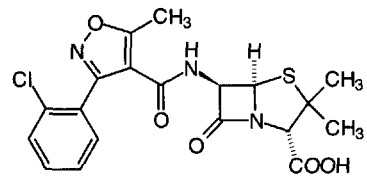


clotting factor *an alternative term for* coagulation factor; *see* **blood coagulation**.

clotting time *an alternative term for* **coagulation time**.

clover-leaf structure one of the models for the secondary structure of **transfer RNA** (tRNA). The nucleotide sequences of different tRNAs can be arranged in similar two-dimensional representations, resembling a clover leaf in shape, in which there are four bihelical regions, containing the maximal number of base pairs, connected by three loops. Some tRNAs have a small extra loop. The clover leaf structure has been largely supported by the tertiary structure of those tRNAs for which structure has been determined by X-ray crystallography.

cloxacillin a semisynthetic penicillin that is resistant to penicillinase and is useful against certain staphylococci.



Clp protease a proteinase/ATPase from *Escherichia coli* with little protein specificity (EC 3.4.21.–). It is a **heat-shock protein** but supposedly a housekeeping proteinase; counterparts occur in many organisms (five motifs). The enzyme is a heterodimer with subunits named from the *clp* genes. The proteolytic subunit is ClpP, database code CLPP_ECOLI, 207 amino acids (23.16 kDa); the ATP-binding subunit is one of ClpA (database code CLPA_ECOLI, 758 amino acids (84.07 kDa)) or ClpX (database code CLPX_ECOLI, 423 amino acids (46.17 kDa)).

CLUSTALV a computer program for the sequence alignment of proteins, *etc.*

cluster **1** a group of iron and sulfur atoms, e.g. Fe_2S_2 or Fe_4S_4, in an iron–sulfur protein. The term is sometimes extended to include other metal atoms, as in the $MoFe_{6\text{-}8}S_4$ cluster in nitrogenase. **2** *or* **cluster of enzymes** *or* **enzyme cluster** the phenomenon of the emergence of new enzymes, or the upsurge of enzymes already present in low concentration, at certain (usually defined) periods along the age axis of the organism.

cluster analysis a method of statistical analysis used, e.g., in **phylogeny** deduced from phenetic characters.

cluster-crystal any of the globular aggregates of calcium oxalate crystals found in some plants.

clustering the occurrence of a number of objects, like or unlike, in clusters; the term is used especially of components of cell membranes, such as receptors.

cm *symbol for* centimetre, i.e. 10^{-2} m.

Cm *symbol for* **1** the carboxymethyl group, $-CH_2-COOH$. **2** curium.

CM *abbr. for* carboxymethyl; e.g. CM-cellulose.

CMAR a gene, cloned from a colon cancer cell line, encoding an 82-amino-acid protein that enhances the attachment of cells to collagen and laminin; the gene is named from cell matrix adhesion regulator. The protein has an N-terminal myristoylation motif (underlined in the partial sequence) and a tyrosine phosphorylation site (bold in the partial sequence), this tyrosine being required for activity. Sequence:

MLRGSDMKGP.....TALRIVEILY.

CMC *abbr. for* **1** critical micellar concentration. **2** carboxymethylcellulose.

CMH *abbr. for* ceramide monohexoside (Cer(Hex) preferred).

CMP *abbr. for* cytidine monophosphate, i.e. cytidine phosphate.

CMR (spectroscopy) *(sometimes) abbr. for* ^{13}C-nuclear magnetic resonance (spectroscopy).

CMU *abbr. for* 3-(*p*-chlorophenyl)-1,1′-dimethylurea; monuron;

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a herbicide that acts by blocking noncyclic photophosphorylation.

^{13}C-NMR (spectroscopy) *abbr. for* carbon-13 nuclear magnetic resonance (spectroscopy).

CNP *abbr. for* C-type natriuretic peptide; it is similar to atrial **natriuretic peptide**.

CNS *abbr. for* central nervous system.

co+ *prefix* denoting **1** together, joint or jointly; in partnership, an equality; to the same degree. **2** *(in mathematics)* of the complement of an angle.

Co **1** *symbol for* cobalt. **2** *abbr. for* coenzyme.

Co I *(obsolete) abbr. for* coenzyme I; *see* **nicotinamide adenine dinucleotide**.

Co II *(obsolete) abbr. for* coenzyme II; *see* **nicotinamide adenine dinucleotide phosphate**.

CoA *symbol for* (free or combined) coenzyme A.

coacervate any viscous phase obtained by **coacervation** of solutions of two or more polymers.

coacervate droplet any of the droplets that, it has been suggested, may have formed in the **primordial soup** by **coacervation** and, perhaps, entrapped primitive catalyst(s); they may have given rise to the first cells. *Compare* **protobiont**.

coacervation any process in which there is a spontaneous separation of a continuous one-phase aqueous solution of a highly hydrated polymer into two aqueous phases, one with a relatively high polymer concentration, the other with a relatively low polymer concentration.

coactone an **ecomone** active in the process of relationship between an active and directing organism and a passive and receiving organism.

coagulant any substance that produces, or aids the production of, coagulation.

coagulase any of a number of serologically distinguishable bacterial enzymes that catalyse the coagulation of citrated or oxalated blood plasma. The extracellular bacterial protein specifically forms a complex with human **prothrombin**; this complex can clot fibrinogen without any proteolytic cleavage of prothrombin. Example from *Staphylococcus aureus*: database code STC1_STAAU, 658 amino acids (74.42 kDa).

coagulase/fibrinolysin precursor *see* **plasminogen activator**.

coagulate **1** to cause a fluid or part of a fluid to change into a solid or semisolid mass by the action of, e.g., heat or chemical substances; to clot. **2** the solid or semisolid mass produced by coagulation. —**coagulable** *adj.*; **coagulation** *n.*

coagulation factors *see* **blood coagulation**.

coagulation time *or* **clotting time** **1** the time taken for a freshly drawn specimen of blood or blood plasma to coagulate (clot) when measured under standard, controlled conditions; it is an indication of the state of the coagulation processes in the specimen. **2** the time taken for a specimen of milk, or of a casein fraction, to coagulate in standard, controlled conditions.

coagulogen a ≈16 kDa fibrinogen-like protein that is found in the hemocyte (amoebocyte) of horseshoe crab (*Limulus polyphemus*) hemolymph and participates in hemostasis. Coagulogen consists of a single, basic polypeptide chain and constitutes about 50% of the protein in horseshoe-crab hemocyte lysates.

coagulum (*pl.* **coagula**) any semisolid coagulated mass or clot, especially that formed by clotting of blood.

coarctation the state of being pressed together or constricted, especially of the aorta or other blood vessel.

coarse descriptive of **1** things that are rough in texture or structure. **2** particles that are large or powders composed of such particles. **3** threads, filaments, or fibres of relatively large diameter. **4** means of adjustment (as of instruments or processes) that provide only inaccurate or gross control, or the adjustments so made.

CoASAc *symbol for* acetyl-coenzyme A.

CoASH *symbol for* (free) coenzyme A.

coated pit an invagination of the cell membrane of many eukaryotic cells, concerned in receptor-mediated selective transport of many proteins and other macromolecules across the cell membrane. During endocytosis it is converted into a **coated vesicle**. The coat is of **clathrin**.

coated-tube method a solid-phase **radioimmunoassay** method in which the specific antibody is immobilized on the inner surface of a small test tube.

coated vesicle a vesicle, formed from a **coated pit**. Observed in the cytoplasm of many eukaryotic cells, coated vesicles measure 50–250 nm in diameter and are characterized by a 'bristle' coat on the outer surface of their lipid membrane. This coat is made up of a polyhedral lattice of **clathrin** subunits together with smaller amounts of other proteins, notably ones of about 100 kDa (**adaptins**), 50 kDa and 20 kDa. Coated vesicles are concerned with the rapid and continuous transport of molecules between specific membranous organelles of the cell and to and from the cell membrane.

coatomer a large protein complex that forms part of the coat of specific Golgi intercisternal transport vesicles that are involved in constitutive vesicular transport between endoplasmic reticulum, Golgi apparatus, and plasma membrane. It has seven subunits known as COPs (from coat protein). COPI-coated vesicles are formed by combination of **ARF** with coatomer. They participate in retrograde traffic from the Golgi apparatus to the endoplasmic reticulum. COPII-coated vesicles are formed from other proteins that include the gene products Sec 13p and Sec 23p. Example: the yeast coatomer is a complex (700–800 kDa); one component is the transport protein product of *SEC21*, database code SC21_YEAST, 935 amino acids (104.71 kDa).

coat protein **1** one of the outer structural proteins of a coated **virus**. **2** any of those subunits of the **coatomer** known as COPs.

cobalamin *the trivial name for* many members of the **vitamin B_{12}** group and their derivatives. A cobalamin is a **cobamide** in which 5,6-dimethylbenzimidazole is the aglycon that forms a link between the cobalt atom and the α1-position of the ribose residue. The sixth position of the cobalt atom may be (artefactually) filled by a variety of groups, e.g. a cyano group giving cyanocobalamin. The oxidation state of the cobalt may be indicated by using a Roman numeral, e.g. cob(I)alamin for Co^{I}.

cob(I)alamin adenosyltransferase EC 2.5.1.17; *other name*: aquacob(I)alamin adenosyltransferase; an enzyme that catalyses the formation of adenosylcobalamin from ATP, cob(I)alamin, and H_2O, with release of orthophosphate and pyrophosphate. The enzyme requires manganese. Example from *Escherichia coli*: database code BTUR_ECOLI, 196 amino acids (21.97 kDa).

cob(II)alamin reductase EC 1.6.99.9; *other name*: vitamin B_{12r} reductase; a flavoprotein enzyme that catalyses a reaction between NADH and two molecules of cob(II)alamin to form two molecules of cob(I)alamin and NAD^+.

cobamide any member of a group of compounds (including the **cobalamins**) that have molecules consisting of a highly substituted tetrapyrrole ring system (corrin) in which a cobalt atom is linked to the four pyrrole nitrogen atoms and with an α-D-ribofuranose 3-phosphate residue attached to one of the side chains.

cobamide coenzyme any of the biochemically active forms of **vitamin B_{12}**. They are **cobalamins** in which either a methyl or 5′-deoxy-5′-adenosyl residue is attached to the sixth position on the cobalt atom.

cocaine 2β-carbomethoxy-3β-benzoxytropane; an alkaloid obtained from dried leaves of the South American shrub *Erythroxylon coca* or by chemical synthesis. It is a cerebral stimulant and narcotic, and has been used as a local anaesthetic. Cocaine acts by blocking neuronal reuptake of, especially, **norepinephrine**, hence its potent vasoconstrictor effects, which can lead to tissue necrosis. Its use is restricted in many countries.

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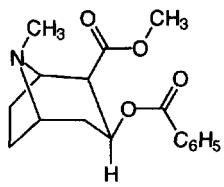


cocaine

cocarboxylase *a former name for* thiamine diphosphate (*see* **vitamin B_1**).

cocarcinogen any noncarcinogenic agent that enhances the effect of a **carcinogen**.

cochromatography a chromatographic technique in which an unknown substance is applied to a chromatographic support together with one or more known compounds, in the expectation that the relative behaviour of the unknown and known substances will assist in the identification of the unknown one.

cocktail a mixture of substances prepared according to a recipe, especially reagent mixtures such as those for use in electrofocusing (**electrofocusing cocktails**), in liquid scintillation counting (**scintillation cocktails**), and in cell-free translation systems (**translation cocktails**). Many such cocktails are commercially available.

COD *abbr. for* chemical oxygen demand.

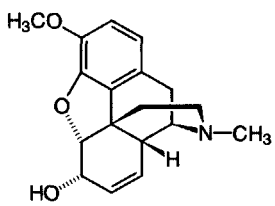
code **1** any system of symbols, together with the rules for their association, that can be used to represent or transfer information; e.g. the **genetic code**. **2** to contain, to be arranged in, or to be expressed through a code; used especially of DNA and mRNA. A gene is said to code for (or encode) its protein product. *Compare* **decoding**.

coded amino acid any of the 20 α-amino acids whose occurrence in proteins is under direct genetic control, i.e. for which a **codon** exists.

codehydrase I *or* **codehydrogenase I** *an obsolete name for* **nicotinamide adenine dinucleotide**.

codehydrase II *or* **codehydrogenase II** *an obsolete name for* **nicotinamide adenine dinucleotide phosphate**.

codeine methylmorphine; (5α,6α)-7,8-didehydro-4,5-epoxy-3-methoxy-17-methylmorphinan-6-ol; an opioid found in opium and manufactured by the methylation of **morphine**. It acts as an agonist at μ, δ, and κ-**opioid receptors** but is generally less potent than morphine, being metabolized in the liver to morphine and norcodeine. It is a narcotic analgesic with **antitussive** activity and is a controlled substance in the US Code of Federal Regulations.



coding ambiguity an adjustment to the prediction of Francis **Crick** that a single nucleotide triplet (codon) would not code for more than one particular amino acid, which was shown by subsequent work to require modification. Thus two codons, AUG and GUG, code not only for the amino acids, methionine and valine respectively, but also are important in chain initiation. Furthermore, there are differences between codon usage in the cytoplasm and mitochondria. In mitochondria UGA codes for Trp rather than chain termination, AUA for Met rather than Ile, and AGA for termination rather than Arg. There is also the problem of proteins containing selenocysteine which is coded by a unique $tRNA^{Sec}$, the codon being UGA which usually codes for termination.

'coding' problem the description given by Francis **Crick** and co-workers in 1957 to the crucial puzzle of the **genetic code**, namely how a sequence employing combinations of only four different nucleotides (i.e. genes) can determine sequences containing combinations of up to 20 different amino acids (i.e. proteins). Crick predicted that groups of three nucleotides would code for each amino acid providing the possibility of 64 codons, more than sufficient for the 20 amino acids. (A binary code of two nucleotides would only provide 16 codons.) The prediction was confirmed with the elucidation of the genetic code in the early 1960s.

coding region *or* **coding sequence** **1** (of a DNA molecule) *an alternative name for* **exon**. **2** (of a messenger RNA molecule) the portion of its complete nucleotide sequence that is translatable into polypeptide.

coding strand the strand in genomic duplex DNA that contains the same sequence of bases as messenger RNA transcribed from the DNA (excepting uracil in RNA in place of thymine in DNA). Its complement is the **noncoding strand**. In some bacteria and viruses, alternate segments of both strands of duplex DNA may be coding, in some instances with overlap. *Other names*: antitemplate strand; codogenic strand; nontranscribing strand; plus strand; sense DNA; sense strand.

coding triplet *or* **coding unit** *an alternative name for* **1 codon**. **2 anticodon**.

cod-liver oil a fish oil obtained from the liver of cod, especially the Atlantic cod (*Gadus morhua*). It is a good source of long-chain *n*-3 **fatty acids**. The typical composition (% total) of major acids is: 16:0, 14%; 16:1 *n*-7, 12%; 18:1 *n*-9, 22%; 20:1 *n*-9, 12%; 22:1 *n*-11, 11%; 20:5 *n*-3, 7%; 22:6 *n*-3, 7%. *See also* **fish oil**.

codogenic strand *an alternative name for* **coding strand**.

codon any group of three consecutive nucleotide bases (base triplet) in a given messenger RNA molecule that, by its composition and sequence, specifies either a particular amino-acid residue in the polypeptide chain synthesized by translation of that messenger RNA, or signals the beginning or the end of the message (i.e. **start codon**, **stop codon**). The term is also used loosely for base triplets in the genomic nucleic acid – in the case of duplex DNA, either on the **coding strand** or **noncoding strand**. For the full set of codons *see* **genetic code**.

coefficient of danger (of a drug or other agonist) the percentage lethal responses to be expected at a dose level that is effective in 95% of trials.

coefficient of variation *or* **coefficient of variability** a parameter used in comparing dispersion in distributions. It is the ratio of the **standard deviation** to the **mean**, i.e. $sx/\bar{x}$. The coefficient of variation is an abstract number independent of the units of measurements; it may also be expressed as a percentage, i.e. $100sx/\bar{x}$.

coefficient of viscosity *see* **viscosity**.

coeliac *a variant spelling (esp. Brit.)* of **celiac**.

coenzyme any of various nonprotein organic **cofactors** that are required, in addition to an enzyme and a substrate, for an enzymic reaction to proceed. Compared with a **prosthetic group** a coenzyme is more easily removed from the **apoenzyme**. The term 'coenzyme' is frequently used imprecisely, although it is now possible to give more informative chemical names to such substances and to define their roles in specific enzymic reactions.

coenzyme I *an obsolete name for* **nicotinamide adenine dinucleotide**.

coenzyme II *an obsolete name for* **nicotinamide adenine dinucleotide phosphate**.

coenzyme A *symbol*: (combined form) CoA *or* (free form) CoASH; 3′-phosphoadenosine-(5′)diphospho(4′)pantetheine; a heat-stable compound that functions as an acyl carrier in a

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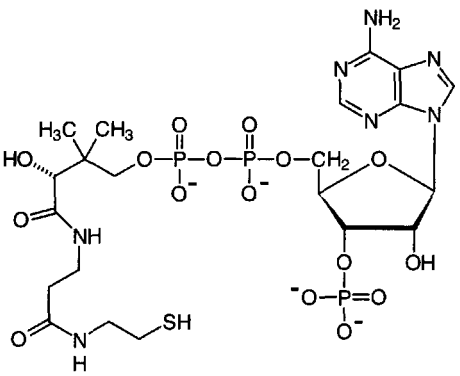
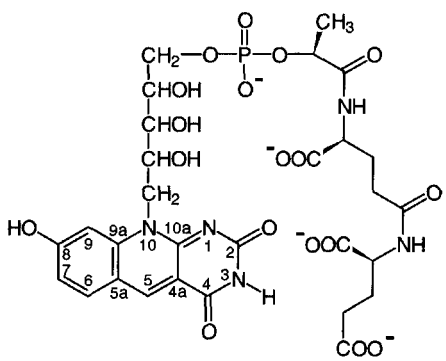
number of biochemical acylation and acyl-transfer reactions, in which the intermediate is a thiol ester. It was originally known as the **acetylation coenzyme**, hence its present name.



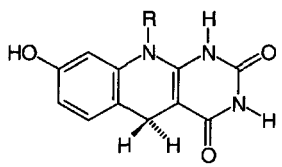
coenzyme C a name sometimes given to a polyglutamate derivative of **tetrahydrofolate**.

coenzyme F *abbr.*: CoF; a name sometimes given to **tetrahydrofolate** or some of its derivatives.

coenzyme F_{420} the *N*-(*N*-L-lactyl-γ-glutamyl)-L-glutamic acid phosphodiester of 7,8-didemethyl-8-hydroxy-5-deazariboflavin that functions as a coenzyme for several oxidoreductases e.g. methylenetetrahydromethanopterin dehydrogenase. It was first found in **methanogenic** Archaea, but later also in other Archaea, and some Bacteria and Eukarya. The oxidized form acts also as a photosensitizer in DNA photolyases. Reduction results in addition of hydrogen at C-1 and C-5, in all cases so far reported being stereospecific for the *Si*-face of the coenzyme.



oxidized form



reduced form (R = substituent at N_{10})

coenzyme F_{430} *see* **factor F_{430}**.

coenzyme factor *an alternative name for* **diaphorase**.

coenzyme M *abbr.*: CoM; 2-thioethanesulfonate, $HSCH_2$–$CH_2SO_3^-$; it is involved as a coenzyme in the pathway of methanogenesis in **methanogenic** bacteria. In the terminal step of the pathway, a methyl group is transferred from methyltetrahydromethanopterin (*see* **tetrahydromethanopterin**) to CoM to form CH_3–S–CoM, from which methane is formed in a reductive step involving **factor F_{430}**.

coenzyme Q *abbr.*: CoQ; *an obsolete name for* **ubiquinone** (the abbreviation Q, is, however, frequently used in diagrams).

coenzyme R *(sometimes) an alternative name for* **biotin**.

CoF *abbr. for* coenzyme F; *see* **tetrahydrofolate**.

cofactor **1** any accessory, nonprotein substance, commonly of low molecular mass, that is necessary for the activity of an enzyme. Metal-ion cofactors have been called **activators**; organic cofactors that are easily removable from the enzyme (e.g. by dialysis) may be called **coenzymes**, but if they are tightly bound they are often termed **prosthetic groups**. *See also* **apoenzyme**, **holoenzyme**. **2** any amino acid that must be present in the medium to allow certain phages to be adsorbed by host bacteria.

cofilin a pH-sensitive nuclear actin depolymerization factor, similar to **destrin** (five motifs in common). Example from pig: database code COFI_PIG, 166 amino acids (18.50 kDa).

cognitive neuroscience the area of neurobiology that aims to explain how the brain enables an animal to interact successfully with its environment. The term cognition has come to refer to that level of description that links molecular science to behaviour.

Cohen, Stanley (1922–) US biochemist; Nobel Laureate in Physiology or Medicine (1986) jointly with R. Levi-Montalcini 'for their discoveries of growth factors'.

coherent *(in physics)* describing two or more waves having the same wavelength and the same phase, e.g. coherent light. The laser is a source of coherent light.

coherent anti-Stokes Raman spectroscopy *abbr.*: CARS; a nonlinear optical technique for obtaining **Raman spectra** with high efficiency. The signal levels, signal-to-noise ratios, resolution, and fluorescence rejection are far better than with normal Raman spectroscopy. CARS can be used for substances at about 1 mM concentration in aqueous solution.

cohesive end *or* **cohesive terminus** *or* **sticky end** the protruding (3′ or 5′) single-stranded terminus on a double-stranded DNA fragment that can associate with a complementary, similarly protruding sequence at the opposite end of the same DNA fragment, or on another fragment, to form a circular, or larger, DNA molecule.

Cohn fractionation a method for the fractionation of human blood plasma proteins to produce minimally altered proteins suitable for clinical use. It involves fractional precipitation with ethanol at temperatures near or below 0°C, with careful control of pH and ionic strength and additions of certain bivalent metal ions, especially Zn^{2+}. The numbered **Cohn fractions** contain the following main constituents: I, fibrinogen; II, γ-globulins; III, β-globulins; IV, α-globulins; V, albumin; VI, glycoproteins. The method has also been applied to the fractionation of plasma proteins of other animals. [After Edwin Joseph Cohn (1892–1953), US biochemist.]

coiled coil *an alternative name for* **supercoil**.

coincidence **1** *(in physics)* the occurrence of radioactive nuclide disintegrations within a time span too short for them to be resolved by a radiation counter. **2** *(in genetics)* the ratio of the number of observed double crossovers to the number expected from the random combination of single crossovers among three or four linked genes.

coincidence correction a correction applied in counting radioactive events for **coincidence losses**, i.e. those events occurring at high count rates when two or more pulses arrive within the resolving time of the counter.

coincidence counter a counter for radioactive events that consists of two opposed detectors and appropriate electronic circuitry so that only those pulses observed by both detectors

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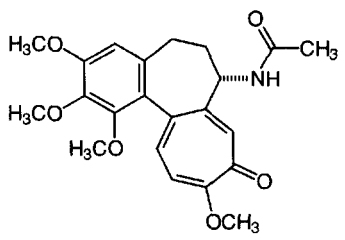
are registered. This arrangement, common in liquid scintillation spectrometers, considerably reduces the number of background counts attributable to random thermionic noise arising in the detectors.

co-ion any ion of low molecular mass present in a colloidal solution or substance that has a charge of the same sign as the (net) charge of a (specified) colloidal ion under particular conditions. *Compare* **counterion**.

colcemide *or* **demecolcine** a derivative of **colchicine** in which the amino group (attached to the non-tropolone seven-membered ring) is methylated instead of acetylated. It binds tubulin and inhibits formation of the mitotic spindle.

colchicine a major alkaloid from the autumn crocus, *Colchicum autumnale* L. It is used experimentally to inhibit the polymerization of **tubulin**, to which it binds specifically and tightly, and to encourage depolymerization of **microtubules**. This action inhibits spindle formation, arrests mitosis at metaphase, and promotes polyploidy in plants. Colchicine also disrupts neutrophil migration and phagocytosis, and inhibits leukotriene B_4 synthesis; it is useful in the treatment of gout. The molecule is noted for a tropolone ring, which is rather rare in natural products. *See also* **colcemide**.



cold **1** of low, or lower than normal, temperature. **2** *(in radiochemistry)* containing no, or an insignificant amount of, a radioactive nuclide; the nonradioactive counterpart of a radionuclide-labelled substance. *Compare* **hot**.

cold agglutinin *see* **cold autoantibody**.

cold autoantibody *or* **cold agglutinin** an antibody that attaches to red cells at low temperatures, reacting better at 4 °C than at 37 °C, and dissociates as the red cells are warmed. Cold autoantibodies are mainly directed against antigens of the **I i system** of blood groups.

cold-insoluble globulin a **cryoglobulin** present in blood plasma or serum. It is normally present at only very low concentrations in human serum but may be elevated in certain rare diseases such as systemic lupus erythematosis. *See also* **fibronectin**.

cold-labile enzyme *or* **cold-sensitive enzyme** any enzyme that, unlike most enzymes, is less stable at 0 °C than at room temperature. In some, but not all, instances activity slowly returns on warming. The phenomenon can be due, e.g., to exothermic dissociation of a stabilizing cofactor from the enzyme or to dissociation into inactive subunits.

cold-sensitive mutation any mutation producing a gene that is functional at a high temperature (the permissive temperature) but inactive at a low temperature (the restrictive temperature). *See* **temperature-sensitive mutation**.

cold-shock protein any of various proteins, synthesized by microorganisms in response to a sudden drop in temperature. These are typically DNA-binding transcription activators, many of which have a characteristic **cold-shock domain** (*abbr.*: CSD); the protein has three motifs. Example from *Escherichia coli*: database code CSPA_ECOLI, 69 amino acids (7.26 kDa). *Compare* **heat-shock proteins**.

coleoptile the protective sheath covering the first leaves of seedling grasses.

colestipol a basic anion-exchange resin that when given orally as the Cl^- form, exchanges anions of chloride in the intestine with those of bile salts, which are then excreted and thus removed from the enterohepatic circulation as an insoluble complex. The resulting reduction in cholesterol absorption culminates in reduced circulating levels of low-density lipoproteins but can increase plasma triacylglycerols. It has therapeutic application in relieving hyperlipoproteinemia.

colestyramine resin *proprietary name*: Dowex 1-X2-Cl; a basic anion-exchange resin that consists predominantly of polystyrene trimethylbenzylammonium chloride. If administered orally, it exchanges anions of chloride with those of intestinal bile salts, which are then excreted as an insoluble complex. The resulting reduction in cholesterol absorption culminates in reduced circulating levels of low-density lipoproteins (LDLs), hence its therapeutic application in relieving hyperlipidemia and LDL-induced hypercholesterolemia.

Col factor *(formerly) an alternative name for* **Col plasmid**.

colforsin *an alternative name for* **forskolin**.

colicin *or (formerly)* **colicine** any member of a range of 40–80 kDa proteins secreted by those strains of the Enterobacteriaceae that kill, but do not lyse, other susceptible strains within this family; a subcategory of **bacteriocin**. Different colicins are designated B, E_1, E_2, I, K, or V, and may be distinguished by their diffusibility and immunogenic and host specificities; their mechanisms of action may vary. They may be coded for by a **Col plasmid**.

colicin factor *or* **colicinogenic factor** *(formerly) an alternative name for* **Col plasmid**.

colicinogenic describing bacteria that are able to produce **colicins**.

colicinogenic factor *see* **Col plasmid**.

coliform **1** describing any bacterium belonging to the genera *Escherichia* or *Klebsiella*. **2** describing any Gram-negative, lactose-fermenting, enteric bacillus or, more loosely, any Gram-negative, enteric bacillus or related organism. **3** any coliform microorganism.

colipase a cofactor of **pancreatic lipase** that inhibits the surface denaturation of lipase and anchors the protein to the lipid–water interface of lipid micelles to prevent inhibition and displacement by bile salts (four motifs). Example (precursor) from human: database code COL_HUMAN, 112 amino acids (11.94 kDa): amino acids 1–17 form the signal; 18–22, enterostatin activation peptide; 23–112, colipase.

coliphage any **bacteriophage** that infects a strain of *Escherichia coli*.

colistin *or* **polymyxin E** a **polymyxin** antibiotic derived from *Bacillus colistinus* and comprising colistins A, B, and C. It acts as a cationic surface-active detergent, disrupting microbial cell wall structure.

colitose 3,6-dideoxy-L-*xylo*-hexose; 3,6-dideoxy-L-galactose; a sugar present in lipopolysaccharide of some strains of *Escherichia coli*. For the D enantiomer, *see* **abequose**.

collagen a group of fibrous proteins of very high tensile strength that form the main component of connective tissue in animals. Collagen is highly enriched in glycine (up to one-third of its amino-acid residues) and somewhat less so in proline plus 3- and 4-hydroxyproline (about 21%); prolines at the third position of the tripeptide repeating unit (G-X-P) are hydroxylated in some or all of the chains. Collagen of bones and skin is metabolically stable, but that of organs such as liver has a high metabolic turnover. Collagens are products of a superfamily of closely related genes found in multicellular animals. The products have been classified into types I to XIII in the order in which they were purified and characterized, and grouped into classes 1 to 4 according to their properties. All contain a typical triple-helical domain formed from three independent chains. Class 1 comprises types I to III, V, and XI. All of these types are fibre-forming, of approximately the same length, having a lengthy uninterrupted collagenous domain with three α chains in the form of a triple helix, and a large globular domain at the C-terminal end. Each of these

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types is synthesized as a procollagen molecule. Several types of α chain are found variously in the different types of class 1 collagen. All of these types aggregate into staggered arrays, first into microfibrils of five collagen molecules that then aggregate into fibres. Class 2 comprises types IX and XII. Type IX was first isolated from pig hyaline cartilage. It is composed of three different α chains, α-1, α-2, αnd α-3 αnd has three short triple-helical domains interrupted by non-collagenous domains.

At the N-terminal end there is a large globular domain. A glycosaminoglycan molecule, chondroitin sulfate, is attached to the α-2 chain. Example from human, α-1 chain (precursor): database code CA19_HUMAN, 931 amino acids (92.97 kDa); residues 1–23 are the signal, and 24–931 the α-1 chain. Type XII was discovered by screening a DNA library and has structural similarities to type IX. The function of these molecules is not known. Class 3 comprises types IV, VI, VII, and X, which serve unique functions. Type IV is the major component of basement membranes. It has long triple-helical domains with a complex globular domain at the C-terminal end. There are six α-x chain isoforms, numbered 1 to 6; example from human α-1 (IV) chain precursor: database code CA14_HUMAN, 1669 amino acids (160.61 kDa); residues 1–27 are the signal, 28–172 a propeptide, and 173–1669 the α-1 (IV) chain. Type VI is a short molecule having a triple-helical domain, 105 nm in length, separating two globular domains. It aggregates into tetramers stabilized by disulfide bonds. Carbohydrate chains consisting of glucosamine, mannose, galactose, fucose, and sialic acid are associated with type VI amounting to 10% of the total mass. Example from *Mus musculus*, α-1 (VI) (precursor): database code CA16_MOUSE, 1025 amino acids (108.49 kDa); residues 1–19 are the signal, 20–1025 the α-1 (VI) chain. Type VII is known as the **anchoring fibril network** and is the largest collagen yet described with a total molecular mass of the precursor of ≈1050 kDa. It has an N-terminal globular domain, a triple-helical domain 424 nm long, and a highly complex C-terminal globular domain. Anchoring fibrils are found within the sub-basal lamina, and appear to anchor the lamina densa to the underlying matrix. Example from human, α-1 (VII) chain (precursor): database code CA17_HUMAN, 2944 amino acids (295.21 kDa); residues 1–16 are the signal, 17–2944 the α-1 (VII) chain. Type X collagen has a restricted tissue distribution, being synthesized mainly by chondrocytes, and is 1438 nm in length. Class 4 comprises types VIII and XIII. Type VIII was first observed as a cell culture product of endothelial cells. It is a 130–140 nm rod found in specialized tissues including the sclera, periosta, perichondria, and cartilage growth plate. Type XIII was identified from a cDNA clone encoding short chains that form a triple-helical domain. Its function is unknown. *See also* **hydroxyproline**.

collagenase any of the proteinases that hydrolyse **collagen**, in particular *Clostridium histolyticum* collagenase (clostridiopeptidase A, EC 3.4.24.3), which preferentially cleaves at Xaa-|-Gly in the sequence

-Zaa-Pro-Xaa-Gly-Pro-Xaa.

It is widely used experimentally in the release of many types of cells from animal tissues, e.g. adipocytes and hepatocytes. *See also* **gelatinase**, **interstitial collagenase**, **microbial collagenase**.

collectin one of a family of plasma **lectins** with a trimeric structure similar to complement C1q.

colligation the formation of a covalent bond by means of two combining groups donating one electron each; the reverse of unimolecular **homolysis**. *Compare* **coordination** (def. 2). —**colligate** *vb.*

colligative property the property of any substance or system (e.g. an ideal solution) that depends only on the number of particles (atoms, molecules, and ions) and not on their nature. For example, gaseous pressure and osmotic pressure are colligative properties.

collimator any device, generally embodying a system of slits and (sometimes) lenses (optical, electric, or magnetic), that is used to produce a nondivergent beam of electromagnetic radiation or particles.

collinear **1** lying in or on the same (straight) line. **2** having a (straight) line in common. **3** describing the state of congruence between the order of amino acids along a polypeptide chain and the order of the corresponding codons along the polynucleotide chain encoding the polypeptide. —**collinearity** *n.*

Collip, James Bertram (1892–1965), Canadian biochemist and endocrinologist notable for his pioneering investigations in endocrinology but particularly for his role in developing (with J. J. R. Macleod) a method for the fractionation of pancreatic extracts to give insulin-containing preparations pure enough to permit the first clinical trials of the hormone to take place; this achievement was duly recognized by Macleod by dividing his share of the Nobel prize with Collip.

collision coupling hormone–receptor–enzyme model a model of enzyme activation summarized by the scheme:

$$H + R + E \overset{K_{mH}}{\rightleftharpoons} HR + E \overset{k_1}{\rightarrow} HRE \overset{k_3}{\rightarrow} HR + E'$$

where H is the hormone, R is the receptor, E is the inactive enzyme, E′ is the activated enzyme, K_{mH} is the hormone–receptor dissociation constant, k_1 is the bimolecular rate constant governing HRE formation, and k_3 is the rate constant governing enzyme activation. In this model the enzymically inactive intermediate, HRE, never accumulates and constitutes only a small fraction of the total receptor and enzyme concentrations.

collision frequency *or* **collision number** the number of collisions per second when there is only one molecule of reactant per cubic centimetre of gas or liquid e.g. in kinetics.

collodion a solution of 4 g pyroxylin (mainly nitrocellulose) in 100 ml of a mixture of 25 ml ethanol and 75 ml diethylether. When exposed to the atmosphere in thin layers it evaporates leaving a tough, colourless film that may be used as a **dialysis membrane**.

colloid *or* **colloidal system** **1** a state of subdivision of matter implying that the molecules or polymolecular particles (the dispersed phase) dispersed in a medium (the continuous phase) have, at least in one direction, a dimension roughly in the range 1 nm–1 μm or that in a system discontinuities are found at distances of this order. All three dimensions need not be in the colloidal range nor is it necessary for the units of a colloidal system to be discrete. Colloids may comprise many individual large molecules such as proteins or polysaccharides, or aggregations of smaller molecules such as colloidal gold. The colloids do not pass, or pass very slowly, through semipermeable membranes. **2** *(in histology)* the structureless substance seen in thyroid gland follicles. —**colloidal** *adj.*

colloidal dispersion any thermodynamically unstable colloidal system in which particles of colloidal size of any nature (e.g. solid, liquid, or gas) are dispersed in a continuous phase of different composition (or state), and which cannot easily be reconstituted after separation of the dispersed phase and the dispersion phase. *Compare* **colloidal solution**.

colloidal electrolyte any electrolyte that gives ions of which at least one is of colloidal size; it includes **polyelectrolytes**.

colloidal solution any thermodynamically stable solution consisting of colloidal macromolecules and solvent that can be easily reconstituted after separation of the macromolecules from the solvent. *Compare* **colloidal dispersion**.

colloid osmotic pressure that part of the osmotic pressure exerted by a solution that is due to dissolved colloids. *See* **osmotic pressure** (def. 1).

colon **1** *(in invertebrates)* the part of the large intestine that extends from the cecum to the rectum. **2** *(in insects)* the second part of the intestine.

colon bacillus *a former term for* ***Escherichia coli***.

colony *(in microbiology)* a circumscribed group of cells, normally derived from a single cell or small cluster of cells, growing on a solid or semisolid medium.

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colony hybridization *or* **colony hybridisation** a blot-transfer method (*see* **blotting**) whereby a very large number of colonies of a bacterium carrying different hybrid plasmids can be rapidly screened to determine which hybrid plasmids contain a specified DNA sequence or gene(s). The bacterial colonies are grown on an agar plate, then replica plated onto nitrocellulose filters. A reference set of the colonies is retained. Then the colonies on the filter are lysed and their DNA is denatured and fixed to the filter *in situ*. The resulting DNA-prints of the colonies are then hybridized to a radioactive RNA probe for the sequence or gene of interest. DNA that binds the probe is then assayed by autoradiography or another detection method, enabling the selection of corresponding colonies from the reference plate.

colony stimulating factor *abbr.*: CSF; any of the **cytokines** that control the differentiation of hemopoietic stem cells, both in the **bone marrow** and in the periphery. The group consists of granulocyte, macrophage, and granulocyte/macrophage CSFs. These promote the development of their specific subsets of leukocytes. **Interleukin**-3 (IL-3), interleukin-5 (IL-5), and **erythropoietin** are also members of this group. IL-3 promotes the differentiation of all the leukocyte lineages, whereas IL-5 is necessary for eosinophil development. Erythropoietin promotes the expansion of erythroid colony forming units. **Granulocyte-colony stimulating factors** (G-CSFs) are cytokines that act in hemopoiesis by controlling the production, differentiation, and function of two related white cell populations: granulocytes and monocytes–macrophages. Example from human (precursor): database code CSF3_HUMAN, 207 amino acids (22.27 kDa). **Granulocyte/macrophage-colony stimulating factors** (GM-CSFs) are cytokine glycoprotein growth factors; they also act in hemopoiesis by controlling the production, differentiation, and function of the granulocytes and the monocytes–macrophages. Example (precursor) from human: database code CSF2_HUMAN, 144 amino acids (16.28 kDa); 3-D structure known. **Macrophage-colony stimulating factor** (M-CSF) is produced by fibroblasts, endothelium, and epithelium; it stimulates growth of macrophage colonies. The molecule is a homodimer; example (precursor) from human: database code CSF1_HUMAN, 554 amino acids (60.05 kDa).

colorimeter a device for measuring colour intensity or differences in colour intensity, either visually or photoelectrically. It is used for quantitative determination of coloured compounds in solutions.

colorimetry any method of quantitative chemical analysis in which the concentration or amount of a compound is determined by comparing the colour produced by the reaction of a reagent with both standard and test amounts of the compound, often using a **colorimeter**.

colostrum the milk secreted by the mammary gland just prior to and for a short period after parturition. It has high levels of protein and immunoglobulin, and its ingestion confers passive maternal immunity on the offspring of some species.

Colour Index *abbr.*: CI; a catalogue of commercially available dyes, identifying each by chemical class, colour, and generic name, and giving their chemical composition where disclosed. Each dye is assigned a five-digit number, prefixed by 'CI'. The preferred trivial name of each dye, its commoner synonyms, and the name(s) of its known manufacturer(s) also are listed.

colour quenching the **quenching** that occurs in liquid scintillation counting due to the absorption of the scintillation emission by the specimen, resulting in a decrease in the light-collecting factor. It can often be reduced by prior bleaching or dilution of the specimen before introduction into the scintillator. *Compare* **chemical quenching**.

Col plasmid *or (formerly)* **Col factor** *or* **colicin factor** *or* **colicinogenic factor** any **plasmid** that carries genetic information for the production of a **colicin**; a subcategory of **bacteriocinogenic factor**.

columbinic acid *or* **ranunculeic acid** (5*E*,9*Z*,12*Z*)-octadeca-5,9,12-trienoic acid; a fatty acid occurring in some seed oils. It can relieve many of the symptoms of essential fatty acid deficiency, although it does not act as a precursor for prostaglandin synthesis.

column an upright cylindrical shaft or tube, especially the tube used to contain the stationary phase in **column chromatography** or **column electrophoresis**, or to contain the packing material in fractional distillation. By extension, the term is also used for the tube (whether vertical, horizontal, or spiral) used in **gas chromatography**.

column chromatography any method of **chromatography** in which the stationary phase is a porous solid contained in a column through which the liquid or gas phase percolates. The principal examples are **adsorption chromatography**, **gel-filtration chromatography**, **gas–liquid chromatography**, and **ion-exchange chromatography**.

column electrophoresis any method of **electrophoresis** in which the support material is contained in a column. Such a technique is usually used for preparative scale separations by **electrofocusing** or **isotachophoresis**.

column volume *symbol*: X; the volume (empty) of that part of a chromatographic column that contains the packing, calculated from the inner diameter and the height or length of the column occupied by the stationary phase under the conditions of use. *Compare* **bed volume**.

CoM *abbr. for* coenzyme M.

combination electrode an electrode comprising a glass electrode and a reference electrode in the same envelope providing a smaller, more compact instrument and ensuring the two electrodes are in the same environment.

combinatorial describing any process that is governed by a specific combination of factors, rather than by any single factor, with different combinations having different effects.

combinatorial chemistry the use of a process to prepare large numbers of structurally diverse sets of organic compounds by combining sets of chemical building blocks (called monomers), often in every possible combination.

combined test of pituitary function a test for suspected hypopituitarism. Insulin, luteinizing hormone-releasing hormone (LHRH), and thyrotropin releasing hormone (TRH) are administered and the response of pituitary hormones is compared with their levels before insulin administration. The lowering of the blood glucose level should stimulate a rise in the blood levels of cortisol and growth hormone; LHRH should increase follicle stimulating hormone (FSH) and luteinizing hormone (LH); and TRH should increase thyrotropin and prolactin.

combining site the site on an **antibody** molecule that combines with the corresponding antigen.

combustion the act or process of burning, especially the quantitative conversion of organic compounds to carbon dioxide and water for elementary analysis, in the estimation of carbon-14 and tritium, or in the determination of a **heat of combustion**.

co-metabolism any oxidation of substances by a microorganism in which the energy yielded by the oxidation is not used to support microbial growth. The presence or absence of growth substrate therefore cannot be inferred from such an oxidation.

command language the language used for giving computers simple instructions. The commands can be assembled into files referred to as batch files (DOS), command files (VMS), or scripts (UNIX).

commensal **1** describing either of two different species of organism that live in close physical association with benefit to one partner but with little effect – either beneficial or harmful – on the other partner. **2** any organism in a commensal association. *Compare* **symbiosis**. —**commensalism** *n.*

committed step *or* **committing reaction** a reaction in a multienzyme reaction sequence (e.g. a metabolic pathway) that once it occurs, causes all the ensuing reactions of the sequence to take place. The sole metabolic role of the committed step is

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to provide precursors of the final product of the pathway; it is usually a physiologically irreversible step.

co-monomer the cross-linking agent added to the monomer in forming the gel used in **polyacrylamide gel electrophoresis**.

COMP *abbr. for* cartilage oligomeric matrix protein; now called thrombospondin-5 (*see* **thrombospondin**).

compactin *an alternative name for* **mevastatin**.

compartment **1** *(in tracer kinetics)* any anatomical, physiological, chemical, or physical subdivision of a system throughout which the concentration ratio of labelled to unlabelled substance is uniform at any given time. It is understood that the rate at which the tracer entering the compartment is mixed with tracer in the compartment is rapid compared with the rate at which the substance leaves the compartment. **2** any subdivision of a model used for the analysis of experimental observations.

compartmentation *or* **compartmentalization** the unequal distribution of a metabolite, enzyme, or metabolic pathway between different parts of a cell (e.g. in cell organelles) or of a whole organism. Consequently only a part of the total of any given chemical present is apparently available for a given reaction. It may refer to morphologically recognizable structures or to **metabolic pools**.

compatibility group *see* **incompatibility group**.

competence **1** the ability of a cell to take up a molecule of exogenously added DNA, and to be transformed by it (*see* **transformation**). **2** the ability of bacterial cells to incorporate phage DNA and to produce phage progeny (*see* **bacteriophage**). **3** the state of reactivity of a cell, tissue, or organism that allows it to respond to specific stimuli by forming new morphological structures or by synthesizing specific proteins (enzymes).

competence factor a secreted protein, or other substance added in culture, that is essential for **competence** in a bacterial or other cell. A 10 kDa basic protein of this type has been isolated from streptococci. It does not bind to DNA but interacts with the cell surface.

competition *(in chemistry)* rivalry between two or more different, but often similar, chemical species for a specific biochemical system, e.g. a receptor, enzyme, transport system, antibody molecule, or ion exchanger.

competition binding *see* **displacement binding**.

competitive antagonism the competition between an **agonist** and an **antagonist** for a receptor that occurs when the binding of agonist and antagonist is mutually exclusive. This may be because the agonist and antagonist compete for the same binding site, or combine with adjacent but overlapping sites. A third possibility is that different sites are involved but that they influence the receptor macromolecule in such a way that agonist and antagonist molecules cannot be bound at the same time. If the agonist and antagonist form only short-lived combinations with the receptor, so that equilibrium between agonist, antagonist, and receptor is reached during the presence of the agonist, the antagonism will be surmountable over a wide range of concentrations (*see* **reversible competitive antagonism**). In contrast, some antagonists, when in close enough proximity to their binding site, may form a stable covalent bond with it (*see* **irreversible competitive antagonism**); the antagonism becomes insurmountable when no spare receptors remain. More generally, the extent to which the action of a competitive antagonist can be overcome by increasing the concentration of agonist is determined by the relative concentrations of the two agents, by the association and dissociation rate constants for their binding, and by the duration of the exposure to each. The action of a competitive antagonist can therefore be surmountable under one set of experimental conditions and insurmountable under another.

competitive inhibition any inhibition of an enzyme activity by an inhibitor that binds to the same active site on the enzyme as does the substrate and when there is no interaction between the inhibitor and the enzyme–substrate complex, nor between the substrate(s) and the enzyme–inhibitor complex. Characteristically, analysis using a Lineweaver–Burk plot reveals that in the presence of a **competitive inhibitor** V_{max} is unchanged and K_m is increased.

competitive inhibitor any inhibitor that produces **competitive inhibition** of the activity of an enzyme. Inhibition produced by a given level of inhibitor can be overcome by an increase of substrate concentration.

competitive protein-binding assay *abbr.*: CPBA; a form of **saturation analysis** in which a naturally occurring proteinaceous binding substance is used.

complement *or (formerly)* **alexin(e)** a system of plasma proteins, found in the blood of vertebrates (and freshly prepared sera), that acts as an effector mechanism in immune defence against infection by microorganisms; the activation products of complement components cause lysis of antigenic cells, attract phagocytic cells to the site of activation, and assist the uptake and destruction of antigenic cells by phagocytes. Complement is also involved in immunological tissue injury. Activity in serum is lost on standing for several days at room temperature or for 30 min at 56 °C. The components of complement, mostly β- or γ-globulins, are generally designated by the symbol C and an identifying suffixed numeral; activated components are indicated by a superscribed bar.

C1, the first component of complement, is a serum proteinase of M_r 400 000 (Sepharose); its concentration in human serum is approximately 250 mg L^{-1}. C1 is a Ca^{2+}-dependent termolecular complex of C1q, C1r, and C1s in the molar ratio of 1:2:2. The C1q subcomponent is composed of nine subunits, six of which are disulfide-linked dimers of the A and B chains, and three of which are disulfide-linked dimers of the C chain. It is one of the few proteins that contain **hydroxyproline** C1r and C1s form a Ca^{2+}-dependent tetramer (M_r 350 000), which is composed of two molecules each of the zymogens C1r (M_r 83 000) and C1s (M_r 83 000). C1r has proteinase activity (EC 3.4.21.41), cleaving Lys(or Arg)–Ile bonds in C1s, which can then activate C2 and C4. Example C1QA: database code C1QA_HUMAN, 705 amino acids (80.08 kDa).

C2, the second component of complement, has an M_r of 110 000 and a concentration in human serum of approximately 15 mg L^{-1}. It is activated by C1s to form C2a and C2b. C2a combines with complement components C2b and C4b to form **C3/C5 convertase**, a serine proteinase (EC 3.1.21.43). C2 is a class II **MHC** protein sequence; example (human, precursor): database code CO2_HUMAN, 752 amino acids (83.14 kDa).

C3, the third component of complement, is a glycoprotein of M_r 180 000; its concentration in human serum is approximately 1200 mg L^{-1}. It activates the complement system, being processed by the removal of four Arg residues to form two chains, α and β, linked by a disulfide bond. C3/C5 convertase activates C3 by cleaving the α chain, releasing C3a anaphylatoxin and generating the α′ chain + β chain of C3b. C3b is split in two positions by complement factor I to form IC3b and C3f. IC3b is then slowly cleaved by factor I to form C3c and C3dg. C3 resembles C4, C5, and **α_2-macroglobulin**. Database code (human, precursor) CO3_HUMAN, 1663 amino acids (186.95 kDa).

C4, the fourth component of complement, has an M_r of 200 000 and a concentration in human serum of approximately 400 mg L^{-1}. The precursor is cleaved enzymatically to form three chains (α, β, and γ); the human form is polymorphic, the allotype being C4a. C4a alleles carry blood group Rogers and C4b alleles carry Chido. Total deficiency of C4a6 allotype is associated with hemolytic disease. C4a anaphylatoxin is a mediator of local inflammatory processes. It induces the contraction of smooth muscle, increases vascular permeability, and causes histamine release from mast cells and basophilic leukocytes. C4 is an MHC class III protein, similar to

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C3, C5, and α_2-macroglobulin. Database code (human, precursor) CO4_HUMAN, 1741 amino acids (192.12 kDa).

C5, the fifth component of complement, is a glycoprotein of M_r 180 000; its concentration in human serum is approximately 80 mg L^{-1}. Activation of C5 initiates the spontaneous assembly of the late complement components, C5–C9, into the membrane attack complex (*see* **MAC** (def. 1)). C5b has a transient binding site for C6. The C5b–C6 complex is the foundation upon which the lytic complex is assembled. The C5 precursor is first processed by the removal of four basic residues, to form two chains, α and β, linked by a disulfide bond. C5 convertase activates C5 by cleaving the α chain, releasing C5a anaphylatoxin and generating the α′ chain + β chain of C5. C5 anaphylatoxin is a mediator of local inflammatory processes. C5a also stimulates the locomotion of polymorphonuclear leukocytes and directs their migration toward sites of inflammation. C5 is similar to C3, C4, and α_2-macroglobulin: database code (human, precursor) CO5_HUMAN, 1676 amino acids (118.12 kDa).

C6, **C7**, **C8**, and **C9**, the sixth, seventh, eighth, and ninth components of complement. These four components, together with C5b, constitute the membrane attack complex; all are related and similar to **perforin**. C6 is a 6S β_2-globulin, and contains nine Cys-rich structural units, believed to be linked by disulfide bonds: database code (human, precursor) CO6_HUMAN, 934 amino acids (104.73 kDa). C7 is a 5.2S β_2-globulin, and serves as a membrane anchor: database code (human, precursor) CO7_HUMAN, 843 amino acids (93.41 kDa). C8 is a γ_1-globulin of M_r 150 000; its concentration in human serum is 10–20 mg L^{-1}. The molecule is a heterotrimer comprising the following subunits: α (human, precursor), database code CO8A_HUMAN, 583 amino acids (64.84 kDa); β (human, precursor), database code CO8B_HUMAN, 591 amino acids (66.87 kDa); and γ (human, precursor), database code CO8B_HUMAN, 202 amino acids (22.19 kDa). C9, a 4.4S α_2-globulin, forms transmembrane channels. It is cleaved by thrombin to form C9a and C9b. Database code (human, precursor) CO9_HUMAN, 559 amino acids (63.09 kDa).

Factor B, a zymogen of M_r 100 000, is activated by factor D, which selectively cleaves an Arg-|-Lys bond when factor B is complexed with C3b to form factor Bb. Following cleavage the C3b–Bb complex acts as **alternative-complement-pathway C3/C5 convertase** (EC 3.4.21.47), which can convert C3 to C3a and C3b by cleaving an Arg-|-Ser bond, and C5 to C5a and C5b by cleavage of an Arg-|-Xaa bond. Database code (human, precursor) CFAB_HUMAN, 739 amino acids (82.91 kDa).

Factor $\bar{D}$, is a serine proteinase (EC 3.4.21.46) of M_r 24 000; its concentration in human plasma is approximately 1.5 mg L^{-1}. Database code (human, precursor) CFAD_HUMAN, 246 amino acids (26.15 kDa); residues 19–246 are factor D.

Factor H (human, precursor: database code CFAH_HUMAN, 1231 amino acids, 138.97 kDa) is a cofactor for **factor I** (EC 3.4.21.45), a serine proteinase that cleaves the α chains of C4b and C3b in the presence of the cofactors for C4-binding; human, precursor: database code CFAI_HUMAN, 583 amino acids (65.65 kDa).

Properdin, a glycoprotein of M_r 220 000, is composed of four, probably identical, noncovalently linked polypeptide chains.

Two alternative reaction cascades for the activation of complement exist. In the so-called **classical pathway**, activation (which requires both Ca^{2+} and Mg^{2+}) is initiated by the binding of the C1q moiety of C1 to the C_H2 regions of antibody molecules in antibody–antigen aggregates or in antibody bound to cells, thus causing C1 to be converted to a proteinase, $\overline{C1}$. $\overline{C1}$ activates C4 and C2 leading to the formation of **C3 convertase**, a complex proteinase, $\overline{C42}$, consisting of the activated components $\overline{C4}$ and $\overline{C2}$. $\overline{C42}$ splits C3 to the chemotactic and anaphylatoxic fragment C3a and the fragment $\overline{C3}$, C3b, which associates with $\overline{C42}$ to give a $\overline{C423}$ complex, **C5 convertase**. The latter is a complex proteinase that in turn splits C5 to $\overline{C5}$ and the chemotactic and anaphylatoxic fragment C5a. In the so-called **alternative pathway**, activation (which requires Mg^{2+} but not Ca^{2+}) is initiated by polysaccharides such as those present on bacterial and yeast cell walls. The proteinase $\bar{D}$ is analogous to $\overline{C1}$ but is normally present in serum, where it causes a continuous slow activation, which is greatly enhanced when polysaccharides are present. $\bar{D}$ acts on B and $\overline{C3}$ to produce $\overline{C3B}$, an alternative C3 convertase. $\overline{C3B}$, which is stabilized by properdin, acts on C3 to produce $(\overline{C3})_n\overline{B}$, an alternative C5 convertase. In both pathways, $\overline{C5}$ production is the last proteolytic step, and there follows a spontaneous association of $\overline{C5}$ with C6, C7, C8, and C9 to form a lytic complex, $\overline{C56789}$. *See also* **lysine(arginine) carboxypeptidase**.

complementarity **1** the interrelationship between one or more units supplementing, being dependent on, or being in a polar position to another unit or units. **2** a reverse correspondence of part of one molecule to part of another molecule, especially of antigen to antibody, enzyme to substrate, or the partners in a **base pair**.

complementary base sequence a sequence in a polynucleotide chain in which all the bases are able to form **base pairs** with a sequence of bases in another polynucleotide chain.

complementary catalysis catalysis in the presence of a prototype molecule, leading to the formation of products with a structure that is in some way complementary to that of the prototype.

complementary DNA *abbr.*: cDNA; a single-stranded DNA molecule that has a **complementary base sequence** to a molecule of a messenger RNA, from which it is produced by the action of **reverse transcriptase** and is used for **molecular cloning**, or as a molecular **probe** (def. 3) in hybridization tests for a specific sequence in cellular DNA. It has the advantage that, unlike genomic DNA, it contains no introns. It must be distinguished from the complementary strand of duplex DNA (*see* **noncoding strand**).

complementary genes any genes that interact to produce a qualitative effect that is distinct from the effects of any one of them separately.

complementary RNA *abbr.*: cRNA; a single-stranded RNA molecule that has a **complementary base sequence** to a specific (chromosomal) DNA sequence (of either strand), from which it is produced by the action of DNA-directed **RNA polymerase**. Naturally occurring cRNA may represent **pre-messenger RNA**, **ribosomal RNA**, or **transfer RNA**. *Compare* **antisense RNA**.

complementary strand (of duplex DNA) *see* **noncoding strand**.

complementation **1** any instance in which the interaction of two incomplete, nonfunctional systems results in a fully functional system. **2** the interaction between viral gene products or gene functions in cells that are multiply or mixedly infected with virus(es), leading to an increased yield of infective virus of one or more parental types. **3** **genetic complementation**.

complementation test any experimental test for **genetic complementation**. *See* ***cis–trans*** **complementation test**.

complement-3 convertase *an alternative name for* C3 convertase; *see* **complement**.

complement-5 convertase *an alternative name for* C5 convertase; *see* **complement**.

complement decay-accelerating factor *abbr.*: DAF; a factor that interferes with catalysis of the conversion of component C2 and factor B of **complement**, and prevents the formation of the amplification convertases of the complement cascade. DAF is expressed on the plasma membranes of all cell types that are in intimate contact with plasma complement proteins, and is a glycosylphosohatidylinositol-anchored protein. Human proteins DAF1 and DAF2 are formed by alternative splicing of a transcript of the same gene. Example (precursor of DAF1) from human: database code DAF1_HUMAN, 440 amino acids (48.66 kDa).

complement fixation *activation of the* ***complement*** *system,*

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characteristically *in vitro* by an antigen–antibody interaction, in which complement components C1 to C9 are activated sequentially.

complement-fixation inhibition test a serological test in which the presence of a substance of known structure either may or may not inhibit the interaction of antibody with complex antigen, and hence also the fixation of **complement**. *Compare* **complement-fixation test**.

complement-fixation test a serological test for the presence of antibody that can fix **complement** on interaction with antigen. The presence or absence of residual complement is detected by an indicator system, e.g. added sheep erythrocytes sensitized with an antibody to sheep erythrocytes. If complement is still present, lysis of the erythrocytes occurs, but if no complement remains, no lysis takes place.

complement receptor any cell-surface receptor that binds activated **complement** components, e.g. the receptor for C3b found on macrophages, neutrophils, and B lymphocytes.

complete Freund's adjuvant *see* **Freund's adjuvant**.

complex 1 any distinct chemical species in which two or more identical or nonidentical chemical species (ionic or uncharged) are associated, usually in stoichiometric proportions, and bound together by weaker interactions than covalent bonds. The term is used for various entities, e.g. coordination complexes, antigen–antibody complexes, enzyme–substrate or enzyme–inhibitor complexes, multienzyme complexes, and receptor–agonist complexes; it is often employed where the precise nature of the interaction is uncertain. **2** to make a complex or incorporate into a complex, especially of a metal ion and a **chelating agent**; to chelate.

complex I, II, III, IV the protein complexes, mainly cytochromes, that with associated ligands including ubiquinone, Fe–S clusters, FMN, FAD, and nicotinamide nucleotides form the mitochondrial electron-transport chain or **respiratory chain**. Each complex can be isolated from the others, and, if suitable substrates and electron acceptors are provided, can function independently in transporting electrons. Complexes I, III, and IV are also involved in proton translocation, a function that requires the complex to be embedded in an orientated environment such as that provided by the intact lipid bilayer of the mitochondrial inner membrane. Purification has led to the identification of the components of each complex. Complex I contains altogether ≈25 different polypeptide subunits including **NADH dehydrogenase (ubiquinone)**, together with FMN and a number of different iron–sulfur clusters containing non-heme iron in the forms Fe–S, Fe_2–S_2, and Fe_4–S_4, the iron of which undergoes oxidation–reduction between oxidation states II and III. The reaction catalysed is the oxidation of NADH by ubiquinone. Complex II contains four subunits of **succinate dehydrogenase (ubiquinone)**, FAD, and iron–sulfur. It catalyses the oxidation of succinate by ubiquinone. Complex III contains ≈10 polypeptide subunits including the four redox centres: cytochrome b_{562}, cytochrome b_{566}, cytochrome c_1, and an Fe_2–S_2 cluster. It catalyses the oxidation of ubiquinol by oxidized cytochrome *c*. The transfer of electrons to cytochrome c_1 involves the **protonmotive Q cycle**. Complex IV contains the 13 polypeptide subunits of cytochrome *c* oxidase, including cytochromes *a* and a_3, and Cu^{2+}. It catalyses the oxidation of reduced cytochrome *c* by dioxygen.

complexation the act or process of forming a (chelate) **complex**, e.g. to render inorganic substances soluble in organic solvents.

complex closed DNA a DNA structure comprising catenated and concatenated circular polynucleotide oligomers. *See* **catenane**, **concatemer**.

complex formation *see* **complex** (def. 2), **complexation**.

complexity *(in molecular biology)* the number of different sequences in DNA as defined by hybridization kinetics.

complexometric titration any titration in which the titrant contains a complexing (chelating) agent that interacts with a metal ion or other chemical species in the test solution, the end point being determined either electrometrically or with an indicator.

complexometry any method for the determination of a metal ion (or other chemical species) involving the formation of a chemical **complex**.

complexone any complex-forming or chelating agent, especially any macrocyclic antibiotic that complexes metal ions.

Complexone *a proprietary name for* **EDTA**.

compound any substance containing two or more identical or nonidentical chemical atoms in fixed numerical proportions and held together by one or more kinds of chemical bond.

compound A, B, C (etc.) *see* **Kendall's compounds**.

compression *see* **band compression**.

Compton, Arthur Holly (1892–1962), US physicist noted for his studies of cosmic rays and X-rays; Nobel Laureate in Physics (1927) 'for his discovery of the effect named after him' [prize shared with C. T. R. Wilson].

Compton effect *or* **Compton scattering** the scattering of photons by free particles that results in an increased photon wavelength (i.e. a decrease in photon energy) and a corresponding increase in the particles' velocity (i.e. an increase in the particles' kinetic energy).

computer-assisted tomography *abbr.*: CAT; *see* **tomography**.

computer of average transients *abbr.*: CAT; an electronic device of many separate channels in which a set of signals (e.g. an NMR spectrum) is repeatedly scanned and the signals stored additively. The stored signals grow linearly with the number of scans but the noise, being random, grows only as the square root of the number of scans taken, thereby improving the signal-to-noise ratio.

COMT *abbr. for* catechol *O*-methyltransferase, EC 2.1.1.6.

comutagen any nonmutagenic agent that enhances the effect of a mutagen.

comutation the occurrence of a mutation near to, and at the same time as, another specified mutation.

con A *abbr. for* concanavalin A.

conalbumin *or* **ovotransferrin** a protein of ≈77 kDa that comprises about 12% of the total solids of egg white. It is distinguishable from **ovalbumin** by its lower thermal coagulation point. It binds Fe^{3+} ions. The amino-acid sequence of conalbumin is probably identical to that of chicken serum **transferrin**, but their carbohydrate moieties are different. Conalbumin precursor, example from *Gallus gallus* (chicken): database code TRFE_CHICK, 705 amino acids (77.76 kDa).

conantokin G *also called* **sleeper peptide**; a toxic peptide from the venom of *Conus geographicus* (fish-hunting cone snail). It is an antagonist of brain **NMDA receptors**. It has the sequence

GEXXLQXNQXLIRXKSN,

where X = γ-carboxyglutamate (Gla). The five Gla residues bind Ca^{2+}.

conarachin a minor globulin occurring, along with **arachin** (def. 1), in seeds of the peanut, *Arachis hypogaea*.

conc. *abbr. for* concentrated.

concanavalin A *abbr.*: con A; an agglutinating and mitogenic protein (*see* **lectin**) that constitutes the major component of the subsidiary globulin fraction (originally named **concanavalin** because it accompanied **canavalin** in purification) obtained from the ripe seeds of the **jack bean**. It is separable from **canavalin** and from the minor component **concanavalin B** by differences in solubility. It is a crystallizable tetramer with 27.5 kDa subunits, dissociating to a dimer below pH 5.8. Each subunit contains one binding site for Mn^{2+} (or other transition metal ion), one for Ca^{2+}, and one for carbohydrate (specifically α-D-mannopyranoses or α-D-glucopyranoses with unmodified hydroxyl groups at C-3, C-4, and C-6); carbohydrate does not bind until the metal binding sites are filled. It agglutinates erythrocytes, and precipitates polysaccharides containing a sufficient number of appropriate terminal residues. It is mitogenic, transforming lymphocytes to blast cells, and can agglutinate some animal tumour cells and inhibit their growth.

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The precursor – database code CONA_CANEN, 290 amino acids (31.49 kDa) – is processed in an unusual way: the mature chain consists of residues 164–281 followed by 30–148; to form a mature chain the precursor undergoes further post-translational modification after removal of the signal sequence; cleavage after Asn at positions 148, 163, and 281 is followed by transposition and ligation (by formation of a new peptide bond) of residues 164–281 and 30–148. The 3-D structure is known (database code NRL_3CNA).

concanavalin B a minor crystallizable protein obtained from ripe seeds of the **jack bean** and separable from **canavalin** and **concanavalin A**.

concatemer *or* **concatenate** originally, an intermediate structure in the biosynthesis of certain DNA viruses, consisting of a number of genomes connected together end to end, and thought to be the immediate precursor to the mature viral genome. The term is now extended to include any linear or circular DNA structure composed of viral genomes joined end to end. The term is also used for circular DNAs which are physically inseparable, one being threaded through the other. *Compare* **catenane**. —**concatemeric** *adj.*

concatenate **1** to join or link together, end to end. **2** joined or linked together. **3** *an alternative term for* **concatemer**. *Compare* **catenate**. —**concatenated** *adj.*; **concatenation** *n.*

concatenated dimer *or* **circular dimer** any circular **concatemer** containing two DNA molecules.

concentrate **1** to reduce the volume of a solution or dispersion by removal of solvent or dispersing medium. **2** to make or become purer or more concentrated by removal of impurities from a substance or material. **3** a concentrated solution or material, especially of foodstuffs, e.g. a vitamin concentrate. —**concentrating** *n.*

concentrated **1** *abbr.*: conc.; *(of a solution, dispersion, or mixture)* containing a relatively high concentration (of a specified solute, kind of dispersed particle, or component); (of substance, particles, etc.) present at relatively high concentration (in a solution, dispersion, etc.). *Compare* **dilute** (def. 1). **2** *(of a solution, dispersion or mixture)* increased in concentration and reduced in volume by removal of solvent, dispersing medium, or admixed material. *Compare* **diluted**.

concentration *abbr.*: concn.; **1 (a) mass concentration** *or* **mass density** *symbol*: ρ or γ; an SI derived physical quantity; it equals the mass of a specified component per unit volume of the system in which it is contained. It is expressed in kg m^{-3}. **(b) amount-of-substance concentration** *or* **amount concentration** *or (in clinical chemistry)* **substance concentration** *symbol*: c; an SI derived physical quantity; it equals the number of moles of a specified component per unit volume of the system in which it is contained. Where there is no risk of confusion the term **concentration** may be used alone. It is expressed in mol m^{-3} or mol dm^{-3}. Amount concentration continues to be expressed often in terms of the litre (*symbol*: l *or* L), which is not an SI unit, although 1 L = 1 dm^3. The older, non-SI, term *molarity* is still commonly used for this quantity; a solution of, say, 1 mol dm^{-3} concentration may thus be referred to also as a 1 molar solution or denoted a 1 M solution, where M is treated as a symbol for mol dm^{-3} (or mol L^{-1}). – *see* **molar** (def. 2). **(c) surface concentration** *symbol*: Γ; an SI derived physical quantity; it equals the number of moles of a specified substance per unit area of the surface at which it is present. It is expressed in mol m^{-2}. **(d) number concentration** *or* **number density** *symbol*: C *or (sometimes)* n; an SI derived physical quantity; it equals the number of specified particles or molecular entities per unit volume of the system in which it is contained. It is expressed in m^{-3}. *Note*: The concentration of a solute in solution may sometimes be expressed in more convenient units esp. in a percentage; e.g. (for solids) as the mass of solute in grams per 100 millilitres of solution (*abbr.*: % w/v), or (for liquids) as the number of volumes of solute per 100 volumes of solution (*abbr.*: % v/v). *See also* **activity** (def. 3), **molality**, **osmolality**, **osmolarity**. **2** the act or process of concentrating. *See* **concentrate** (def. 1, 2).

concentration equilibrium constant any **equilibrium constant** expressed in terms of concentrations rather than activities.

concentration gradient the change of concentration with distance, e.g. the change in concentration of a solute across a membrane or along a gradient.

concentration of enzymic activity *(obsolete) see* **enzymic activity**.

concentration polarization *(in membrane ultrafiltration)* the accumulation of retained macrosolutes on the membrane, forming a secondary membrane, that results in restriction of transport through the filter and alteration of selectivity, which may lead to rejection of normally permeating species.

concentration quenching the **quenching** of fluorescence that becomes significant when the fluor concentration is increased beyond a certain point. It is of importance, e.g., in liquid scintillation counting and in experiments involving the introduction of fluorescent groups (probes) into macromolecules.

concentration ratio *or* **dose ratio** *symbol*: r; the ratio of the concentration of an agonist that produces a specified response (often but not necessarily 50% of the maximal response to that agonist in an assay) in the presence of an antagonist, to the agonist concentration that produces the same response in the absence of antagonist.

concentric cylinder viscometer *an alternative name for* **Couette viscometer**.

concerted reaction any chemical reaction in which two chemical processes occur within the same reaction step; i.e. one in which a new chemical bond is formed at the same time as, and as a direct result of, the breaking of another chemical bond.

concerted symmetry model a model of ligand binding to oligomeric proteins in which the characteristic assumption is that molecular symmetry of the **oligomer** is conserved so that only two states are accessible to it: either with all the **protomers** in the first conformational state or all the protomers in the second state. *See* **Monod–Wyman–Changeux model**.

concerted transition the simultaneous transition of all identical subunits (i.e. protomers) of an oligomeric molecule from the first conformational state to the second state and vice versa, as is required in any **concerted symmetry model** for allosteric proteins.

concn. *abbr. for* concentration.

concordance *the condition in which both members of a twin pair demonstrate the same phenotype or trait.*

condensate any product of a **condensation**, especially a liquid from a gas or vapour.

condensation **1** the act or process of condensing; the state of being condensed. **2** the product of condensing; a condensed mass. **3** any (usually stepwise) chemical reaction in which two or more identical or nonidentical molecular entities, or two parts of one entity, combine with the elimination of a molecule of water, ammonia, ethanol, hydrogen sulfide, or other simple substance. The combining entities or parts each (formally) contribute a moiety to the molecule eliminated.

condensation polymerization a polymerization by repeated condensation, i.e. with elimination of some simple substance, to form a **condensation polymer**.

condense **1** to make or to be made more compact or denser. **2** to change or cause to change a gas or vapour to a liquid or solid. **3** (of a compound) to undergo or cause to undergo a **condensation** (def. 3).

condensed **1** converted to a dense or denser form; e.g. **condensed DNA** in **nucleosomes** or in the early stages of maturation of T-even phages; or the **condensed form of mitochondria** in which the cristae are swollen, the matrix volume is much reduced, and the inner membrane space is increased. **2** reduced from the gaseous to the liquid state.

condenser **1** any device for converting a gas or vapour into a liquid (or solids) by cooling. **2** a lens or set of lenses that con-

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centrates light into a small area. **3** *a former name for* capacitor; an electrical component that stores electric charge.

condensing enzyme **1** citrate condensing enzyme, EC 4.1.3.7; *see* **citrate (*si*)-synthase**. **2** β-oxoacyl-ACP synthase, EC 2.3.1.41; 3-oxoacyl-[acyl-carrier-protein]synthase (*see* **fatty acid synthase complex**).

conditional association constant *or* **conditional stability constant** an **association constant** determined in conditions similar to those in which the reaction under consideration is taking place, e.g. in the internal milieu of a cell.

conditional lethal mutation any mutation that produces a mutant (**conditional lethal mutant**) whose viability depends on the conditions of growth. It grows normally in permissive conditions but in restrictive conditions it does not grow, thereby expressing its lethal mutation. *See*, e.g., **temperature-sensitive mutation**.

conduct to allow the passage of electricity, heat, or electromagnetic radiation.

conductance *see* **electric conductance**.

conductance water *an alternative name for* **conductivity water**.

conductimetric *or* **conductiometric** *a variant spelling of* conductometric; *see* **conductometry**.

conductimetry *or* **conductiometry** *a variant spelling of* **conductometry**.

conduction **1** the transfer of heat or electricity through a material. **2** the transmission of an impulse, either electrical or chemical, along a nerve fibre.

conductivity **1 electrical conductivity** *symbol*: κ; a measure of the ability of a material to conduct an electric current or impulse. It is defined as the reciprocal of the resistivity of the material, and is expressed in siemens m^{-1}. *See also* **electrolytic conductivity**. **2 thermal conductivity**.

conductivity water *or* **conductance water** very pure water, of electrolytic conductivity $<1 \times 10^{-4}$ siemens m^{-1}.

conductometric titration any titration in which the end point is indicated by an inflection in the curve of conductivity against volume of titrant added. For instance when an HCl solution is titrated with an NaOH solution, the conductivity decreases as the faster moving H_3O^+ ions are replaced by slower moving Na^+ ions; after the equivalence point the conductivity increases as the concentration of the fast-moving OH^- ions increases.

conductometry *or* **conductimetry** *or* **conductiometry** any method of chemical analysis based on measurements of electrical conductivity. —**conductometric** *adj.*

conductor any substance or system that allows the passage of electricity, heat, or electromagnetic radiation.

cone cell *or* **cone** one of the two types of light-sensitive cell of the vertebrate retina (*compare* **rod cell**). Cone cells are conical or flask-shaped, and contain the photopigment **iodopsin** or (in freshwater and migratory fishes and some amphibians) **cyanopsin**. They are responsible for photopic (daylight) vision; and are densest in the fovea and absent from the margin of the retina. Human cone cells are thought to be of three types, each containing an iodopsin of different spectral sensitivity; hence they are responsible also for colour vision.

confidence limits *(in statistics)* the upper and lower limits of the range of values within which the true mean is expected to lie, on the basis of an estimate of the mean obtained from a sample of values. The confidence limits vary according to the (specified) probability that they will be correct.

configuration classically, the arrangement of the atoms of a molecule in space, without regard to arrangements that differ only as after rotation about one or more single bonds; the term is now sometimes limited so that no regard is paid to π-bonds or to bonds of a partial order between one and two, and sometimes further limited so that no regard is paid to rotation about bonds of any order, including double bonds. Interconversion of molecules of different configurations requires the formal making and breaking of covalent bonds, no account being taken of changes to hydrogen bonds. *Compare* **conformation**. *See also* **absolute configuration**, **pyrimidine dimer**. —**configurational** *adj.*

configurational base unit (of a polymer) a **constitutional base unit** of the polymer whose configuration is defined at the minimum at one site of steric isomerism in the main chain of the polymer.

configurational block a **block** in a polymer containing only one species of **configurational base unit**.

configurational inversion *see* **racemize**, **Walden inversion**.

configurational isomer any of two or more isomers that differ only in stereochemical **configuration**.

confluence *(in cell culture)* the state reached when one or more cells or groups of cells, grown in culture on (so-called) solid medium, have multiplied to cover the surface of the medium completely but without overlying each other. —**confluent** *adj.*

confocal microscope a microscope that produces a series of images, often called optical sections, that have much better resolution than images of the same specimens obtained using conventional epifluoresence light microscopy. Such a microscope depends on laser light focused through a pinhole onto a single point in the specimen. From a succession of such images a 3-D image can be created. This is primarily used in biological imaging for mapping the distribution of fluorescently labelled macromolecules, such as antibodies, in various tissues.

conformation the various arrangements of the atoms of a molecule (of defined **configuration**) in space that differ only as after rotation about single bonds; the term is now sometimes extended to include rotation about π-bonds or bonds of partial order between one and two, and sometimes further extended to include also rotation about bonds of any order, including double bonds. Interconversion of molecules of different conformations does not involve the breaking and making of chemical bonds (except hydrogen bonds) or changes in **chirality**. The following special terms and symbols distinguish different possible conformations of various classes or portions of molecules.

(1) **Cyclic compounds**. Nonplanar six-membered rings may exist in **boat conformation**, **chair conformation**, **half-boat conformation**, **half-chair conformation**, **skew conformation** (def. 1), or **twist conformation** (def. 1); and nonplanar five-membered rings may exist in **envelope conformation** or **twist conformation** (def. 2). For a six-membered or five-membered ring form of a monosaccharide or monosaccharide derivative these conformations may be designated by the following conformational descriptors suffixed to their chemical names: *-B*, boat; *-C*, chair; *-E*, envelope; *-H*, half-chair; *-S*, skew; *-T*, twist; the locants of the ring atoms that lie above and/or below the reference plane, when the numbering appears clockwise, may be added to these symbols as left superscripts and/or right subscripts, respectively. A bond to a tetrahedral atom in a six-membered ring is termed **axial** (*abbr.*: a) if it or its projection makes a large angle with the plane containing a majority of the ring atoms, and **equatorial** (*abbr.*: e) if this angle is small; the same terms are applied to atoms or groups attached to such bonds. The corresponding terms for a bond from an atom directly attached to a doubly bonded atom in a monounsaturated six-membered ring are **pseudoaxial** (*abbr.*: a′) and **pseudoequatorial** (*abbr.*: e′), respectively.

(2) **Nucleotides**. When atom C-2′ or C-3′ of the ribo- or deoxyribofuranose ring of a nucleotide lies out of the plane of the other four ring atoms, the ring conformation is designated by the descriptor *endo-* if either atom lies above the ring, i.e. towards the nitrogenous base, and by the descriptor *exo-* if it lies below the ring, i.e. away from the base. In addition the base and sugar rings may be in either of two relative positions: the conformation is said to be **anticlinal** (*abbr.*: *anti-*) if the groups at positions 2 and 3 of a pyrimidine residue or positions 1, 2, and 6 of a purine residue lie away from the sugar ring, and **synclinal** (*abbr.*: *syn-*) if these groups lie over the sugar ring.

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(3) **Torsion angle**. If rotation about a given bond in a molecule is restricted for any reason, the conformation of atoms or groups about that bond may be described by the **torsion angle** (*symbol*: θ). When, in a **Newman projection**, two atoms or groups attached at opposite ends of a bond appear one more or less directly behind the other, i.e. $\theta \approx 0°$, these atoms or groups are termed **eclipsed**, and that portion of the molecule is described as being in the eclipsed conformation. If not eclipsed (in an ideal case, when all torsion angles equal 60°), the atoms or groups are termed **staggered**, and the molecule is described as being in the staggered conformation; such a conformation is termed **synperiplanar** (*abbr.*: *sp*) (or sometimes *cis* (*abbr.*: c)), **synclinal** (*abbr.*: *sc*) (or sometimes *gauche* (*abbr.*: g) or *skew*), **anticlinal** (*abbr.*: *ac*), or **antiperiplanar** (*abbr.*: *ap*) (or sometimes *trans* (*abbr.*: t)) according as the torsion angle is, respectively, within ±30°, ±60°, ±120°, or ±180° of 0°, the torsion angle being defined according to specified criteria. (*Note*: Because the terms *cis* and *trans* have other meanings, their use in this context is not recommended.) —**conformational** *adj.*

conformational analysis the application of a set of specific rules to determine the conformation of a molecule in which the strain will be minimal, i.e. the most stable and preferred conformation of the molecule.

conformational change **1** any change in conformation **2** any change in the three-dimensional structure of a macromolecule, membrane, or other entity.

conformational-coupling hypothesis a hypothesis (now superseded) that the energy yielded by the processes of electron transport, e.g. in mitochondria, is conserved in the form of a conformational change in an electron carrier protein or in the coupling factor (F_1 ATPase) molecule. The high-energy conformational state results from an energy-dependent shift in the number and location of weak bonds that maintain the three-dimensional conformation of the protein. The energy inherent in this 'energized' conformation is thought to be used to cause the formation of ATP from ADP and inorganic phosphate. This hypothesis was put forward after attempts to find a high-energy intermediate that coupled electron transport to oxidative phosphorylation, failed. It has been superseded by the **chemiosmotic coupling hypothesis**.

conformational formula a diagrammatic representation on a plane surface of the structural formula of a molecule that shows the relative dispositions in space of the constituent atoms or groups. Such representations are used especially to depict instances of conformational isomerism. For a monosaccharide or monosaccharide derivative, the conformational formula may be combined with a **Haworth representation**. *See also* **Newman projection**.

conformational isomer *or (sometimes)* **conformer** any of two or more isomers that differ only in their stereochemical **conformation**.

conformational map *an alternative name for* **Ramachandran plot**.

conformer **1** a molecule in a conformation into which its atoms return spontaneously after small displacements. **2** *an alternative term for* **conformational isomer**.

conformon a quantized energy package that, according to the **conformational-coupling hypothesis**, is associated with a localized conformational change in a protein in the mitochondrial membrane.

congener **1** any member of a (specified) group. **2** *(in taxonomy)* any member of a specified genus. **3** *(in chemistry)* **a** a chemical substance related to another, e.g. as a derivative or as an element of the same group of the periodic table. **b** a secondary product retained in an alcoholic beverage (or extract of a natural product) that contributes significantly to the final characteristics of the beverage (or the extract).

congenic of, or pertaining to, a **congener**; **homogenic**.

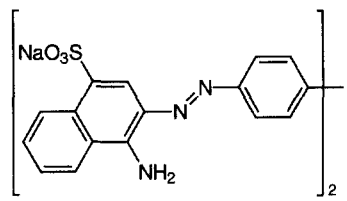
congenital describing a character or trait (phenotype) that exists at or dates from birth. It neither includes all inherited conditions nor excludes characters resulting from environmental causes.

congenital adrenal hyperplasia a syndrome embracing a group of inherited enzyme deficiencies of adrenal steroid hormone biosynthesis. A deficiency of 21-hydroxylase (steroid 21-monooxygenase, EC 1.14.99.10) accounts for the great majority of cases; it leads to failure to synthesize cortisol and results in overproduction of ACTH (due to release from negative feedback by cortisol) and consequently there is hyperplasia of the adrenal and overproduction of 17-hydroxyprogesterone and androstene 3,17-dione by overstimulated alternative pathways. Deficiency (usually partial) of 11β-hydroxylase (steroid 11β-monooxygenase, EC 1.14.15.4) accounts for most other cases; in this condition, 11-deoxycorticosterone accumulates. Very rarely, deficiency of 17-hydroxylase (steroid 17α-monooxygenase, EC 1.14.99.9) or 18-hydroxylase (corticosterone 18-monooxygenase, EC 1.14.15.5) may occur.

conglutination the agglutination of bacterial or red blood cells, that have been sensitized with specific antibody, in the presence of (nonhemolytic) **complement** and **conglutinin**.

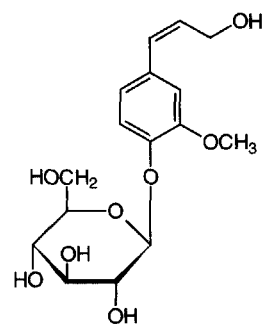
conglutinin a nonimmunoglobulin protein, present in the plasma of cattle and other bovids, that aggregates **complement**-coated immune complexes or cells.

Congo Red sodium diphenyldiazo-bis-α-naphthylaminesulfonate; CI 22120; Direct Red 28; an indicator dye that is blue-violet at pH 3.0 and red at pH 5.0. It is used for detecting and estimating free HCl in gastric contents, as an addition to culture media, and for staining **amyloid**.



Congo Red fibrin a preparation obtained by heating fibrin to 80 °C in a slightly alkaline Congo Red solution and thoroughly washing. It was formerly used in the detection of proteolytic activity since the dye does not dissolve in aqueous solutions unless the fibrin is digested.

coniferin 4-(3-hydroxy-1-propenyl)-2-methoxyphenyl β-D-glucopyranoside; the major **glycoside** present in conifers and some other plants.



coniferyl alcohol the aglycon of **coniferin**; it occurs as a building unit of plant **lignins**.

coniine 2-propylpiperidine; the toxic alkaloid of poison hem-

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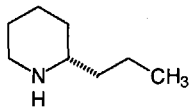
lock, *Conium maculatum*. The natural enantiomer has *S* configuration.



conjugase γ-Glu-X carboxypeptidase, EC 3.4.19.9 (formerly EC 3.4.22.12); γ-glutamyl hydrolase; an enzyme that hydrolyses γ-glutamyl bonds in *N*-pteroyl-γ-oligoglutamate, pteroyl-γ-diglutamate being a prominent product.

conjugate **1** to effect or undergo **conjugation**. **2** describing either of a pair of interconvertible substances, e.g. a **conjugate acid–base pair**. **3** the product formed as a result of conjugation.

conjugate acid–base pair the relationship between two chemical species, BH^+ and B, that are related by the reaction: $BH^+ = B + H^+$. Then BH^+ is the **conjugate acid** of the base B, B is the **conjugate base** of the acid BH^+, and BH^+ and B are a conjugate acid–base pair.

conjugate base *see* **conjugate acid–base pair**.

conjugated **1** describing a compound that is formed by the linking of two compounds. **2** displaying or having undergone **conjugation**.

conjugated double bond any of two or more double bonds in a molecule where each double bond is separated from the next one by one single bond. *Compare* **conjugation** (def. 2).

conjugated protein any protein that contains a nonprotein component, often in stoichiometric proportion. The nonprotein component may be a metal ion, a lipid, a carbohydrate, or a nucleic acid, and may be either loosely or tightly bound to the polypeptide chain(s).

conjugation **1** the act of joining together; the state of being joined together. **2** an alternating sequence of multiple and single chemical bonds containing at least two multiple bonds with delocalization of pi-electrons and resultant additional chemical stability. **3** the covalent or noncovalent joining together of one (larger) molecule, e.g. a protein or bile acid, with a second (smaller) molecule. **4** a process of sexual reproduction occurring in various types of unicellular organisms. In bacteria, e.g. *Escherichia coli*, it involves the transfer of DNA from a donor cell to a recipient cell via a sex **pilus**; in protozoa, e.g. *Paramecium aurelia*, a true exchange of DNA occurs between the participating cells, which belong to different mating types.

conjugation labelling a procedure for introducing a **label** into a large molecule of interest by covalently coupling it, in a specific chemical reaction, to a small molecule containing the label (*see* **conjugation** (def. 3)). It is particularly useful for labelling with radioiodine any protein or peptide that is sensitive to oxidative procedures or to noxious components of commercial radioiodine, that lacks tyrosine residues reactive to iodine, or that requires to be labelled at a residue other than tyrosine. *See also* **Bolton and Hunter reagent**.

conjugative plasmid any **plasmid** that can bring about the transfer of DNA by **conjugation** (def. 3).

conjugon any genetic element that is required for bacterial **conjugation** (def. 4), e.g. **fertility factor**.

connective tissue any supporting tissue that lies between other tissues and consists of cells embedded in a relatively large amount of extracellular matrix.

connective tissue growth factor *abbr.*: CTGF; a growth factor of testis, spleen, kidney, lung, heart, and brain, that is similar to **CEF10**; one of a family of growth regulators that belong to a group of immediate-early genes expressed after induction by growth factors or certain oncogenes. The family includes **Cyr61**, βIG-M1, and βIG-M2. Example (precursor) from mouse: database code CTGF_MOUSE, 348 amino acids (37.75 kDa).

connectivity *(in chemistry)* the information in any molecular formula or model regarding the order in which the constituent atoms of the molecule are linked, irrespective of the nature of the linkages.

connexin the main protein component of a **connexon**. Each connexin contains four putative membrane-spanning α-helices, and six connexins make up each connexon. A number of different subtypes of connexin exist within each species, contributing different functional behaviour to different connexons. Example from human: database code CX26_HUMAN, 208 amino acids (24.27 kDa); four motifs.

connexon the structural subunit of a **gap junction**, the structure that forms a bridge between adjacent cells in certain tissues of vertebrates. Seen by electron microscopy or low-angle X-ray diffraction, an individual gap junction consists of a number ($10–10^4$) of connexons, often in hexagonal array, embedded in and protruding from either side of each of the opposed cell membranes in register and linked to one another. Each connexon is a cylindrical proteinaceous structure, about 6–8.5 nm in diameter and 7.5 nm long; it consists of six rod-shaped, essentially rigid subunits (**connexins**) of about 25 kDa arranged in an annulus. The diameter of the central opening can apparently be varied by radial displacement of the subunits at their cytoplasmic extremities. Each connexin spans one cell membrane, two with connecting ends being required to form a channel across both membranes. Such channels provide a regulable hydrophilic pathway permitting the passage of small molecules (up to about 800 Da) between adjacent cells; the specificity of each channel is determined by the type of connexin it utilizes.

conotoxin *abbr.*: ω-CT; any of several peptides of the family of ω-conotoxins isolated from the venoms of two marine snails, *Conus geographicus* and *C. magus*. All ω-conotoxins have a conserved pattern of cysteine residues linked by four disulfide bridges. They are neurotoxins that inhibit voltage-gated Ca^{2+} channels and neurotransmitter release. ω-Conotoxin GVIA has the structure:

[tricyclic (1→16, 8→19, 15→26)(H-Cys^1-Lys-Ser-Hyp-Gly-Ser-Ser-Cys^8-Ser-Hyp-Thr-Ser-Tyr-Asn-Cys^{15}-Cys^{16}-Arg-Ser-Cys^{19}-Asn-Hyp-Tyr-Thr-Lys-Arg-Cys^{26}-Tyr-NH_2)].

consensus sequence an idealized sequence of nucleotides, or their constituent bases, or amino acids, base, or amino acid that represents the nucleotide most likely to occur at each position in the sequence. Consensus sequences are used to identify RNA splicing sites, other sites, plasmids, and families of proteins.

conservation the retention of structure by a macromolecule, or by a specified segment of one, with variation of circumstance (environmental, genetic, etc.). When used of primary structure, it can be synonymous with **sequence homology**. The degree of retention of structure is usually specified. *See also* **conserved**.

conservation of energy (law of the) *see* **thermodynamics**.

conservative base change *or* **conservative base substitution** any mutational change, including substitution of a base, in a particular base triplet in a DNA molecule such that either the amino acid encoded by that base triplet is not altered, or there is no major change in the properties of the R group of the amino acids involved, e.g. Glu for Asp. *See* **genetic code**, **wobble hypothesis**.

conservative replacement *or* **conservative substitution** any replacement or substitution in a polypeptide chain of a particular amino acid residue by another one with similar properties, e.g. Arg for Lys, Phe for Tyr, Glu for Asp.

conserved describing a tendency to invariance in corresponding residues or sequences of residues of encoded macromolecules (e.g. proteins) obtained from specimens of genetically different sources. Macromolecules showing a high degree of

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invariance of their primary structure are said to be highly conserved; ones exhibiting considerable variation are described as poorly conserved. *See also* **conservation**, **homologous**.

constant region the region of a chain of an **immunoglobulin** molecule that is characterized by invariability of the amino-acid sequence from molecule to molecule, apart from certain residues at allotypic marker sites. The constant region of the light chain (corresponding to the C-terminal part) is designated C_L, while the constant region of the heavy chain is designated C_H. Within a constant region, individual domains may be further designated C_H1, C_H2, etc. In a more precise designation of a heavy chain the 'H' subscript is replaced by the Greek letter corresponding to the type of heavy chain that defines the particular class of immunoglobulins. Hence, the constant region of an **immunoglobulin G**, in which the heavy chain is designated γ, can be designated $C_\gamma1$, $C_\gamma2$, etc.

constitutional base unit the smallest possible regularly repeated unit (i.e. identical group of monomers) of a regular **polymer**.

constitutional block a **block** of a polymer that contains only one species of **constitutional base unit**.

constitutional isomer *or (formerly)* **structural isomer** any of two or more **isomers** that differ in their molecular constitution, i.e. in the nature and sequence of bonding of their atoms rather than in the arrangement of their atoms in space. For example, ethanol, CH_3–CH_2–OH, and dimethyl ether, CH_3–O–CH_3, are constitutional isomers. *Compare* **stereoisomer**.

constitutive enzyme any enzyme that is formed at a constant rate and in constant amount in a given cell, regardless of the metabolic state of the cell or organism. *Compare* **induced enzyme**.

constitutive genes genes that are expressed following interaction between a promoter and RNA polymerase without additional regulation. *Also known as* **housekeeping genes**, they are expressed in virtually all cells since they are essential for the cell's activity.

constitutive mutation any mutation that results in an increased constitutive synthesis (i.e. synthesis as if by a **constitutive gene**) by a prokaryote of several functionally related, inducible enzymes. In such mutations either an operator gene is modified so that the repressor cannot combine with it or the regulator gene is modified so that the repressor is not formed.

contact amino acid any of the amino-acid residues in the **active site** (def. 1) of an enzyme that are at some stage within one bond distance of some point on the substrate molecule in the enzyme–substrate complex. They may include both catalytic residues and specificity residues. *Compare* **auxiliary amino acid**.

contact hypersensitivity a form of immunological **hypersensitivity**, immediate or delayed, that is provoked in the skin or mucous surfaces by contact with specific agents acting as either antigens or haptens.

contact inhibition a phenomenon, seen in cultures of normal eukaryotic cells, in which cell division is inhibited by cell-to-cell contact. When one cell contacts another cell as a result of increased cell density, it first ceases to move, then metabolizes more slowly and ceases to divide. An outstanding feature of malignant cells is their loss of contact inhibition so that they multiply unchecked. *See also* **transformation** (def. 2).

contact residue *see* **contact amino acid**.

contact sensitivity the ability of an organism to respond to a biocide, e.g. an insecticide or a selective herbicide, applied to the integument.

containment the use of any structural or procedural safeguards to minimize the possible risks, to the experimenter or to the environment, in hazardous or potentially hazardous operations, especially genetic manipulations or the use of ionizing radiation.

contamination the presence of any contaminant; the act of introducing a contaminant; pollution; the presence of harmful or invasive microorganisms in a population of desirable ones. *Compare* **decontamination**.

context **1** any parts of a piece of writing or speech that precede or follow a specified word or passage and contribute to its full meaning. **2** *(in mycology)* the layers that develop between the hymenium and the true mycelium in certain fungi.

context effect any effect of nucleotide residues outside a codon in an mRNA molecule in influencing the efficiency of the reading of that codon by the appropriate tRNA molecule. *Compare* **context** (def. 1).

context mutation any mutation that brings about an alteration in the **context effect** of nucleotide residues outside a particular **codon** in an mRNA molecule.

contig one of a set of overlapping clones that represent a continuous region of DNA. Each contig is a genomic clone, usually in a **cosmid** or a **YAC**. They are used in **contig mapping**.

contig mapping a technique used in projects such as the Human Genome Project to enable the physical map of (part of) a chromosome to be determined. The method relies on the use of overlapping clones, referred to as **contigs**.

contiguous gene syndrome any of the complex disease phenotypes associated with a chromosomal microdeletion affecting multiple, unrelated genetic loci physically contiguous on a chromosome.

continuous culture any cell culture in which the cells are in the growth phase over a prolonged period of time. *See also* **chemostat**.

continuous distribution any nonquantized distribution; e.g. in a large population one measurement, x, may be considered to vary continuously, and the probability, y, of the occurrence of a particular value of x is given by $y = f(x)$.

continuous epitope an immunological determinant (i.e. **epitope**) on an antigen that is formed from a single linear stretch of amino acids. It is much less common than a **discontinuous epitope**.

continuous-flow centrifugation any preparative centrifugation technique, used for collecting materials from relatively large volumes of liquid, in which a liquid is continuously fed into a rotor, the sediment is collected, and the supernatant is withdrawn continuously as the rotor rotates. *See* **centrifugal elutriation**, **Sharples supercentrifuge**, **zonal centrifugation**.

continuous-flow electrophoresis a method of electrophoresis in which the protein (or other) solution is applied continuously to an inert support such as paper (then usually called **curtain electrophoresis**) or glass beads or is allowed to flow between two closely spaced parallel plates. The solution flows down the support by gravity and an electric potential applied at right angles causes migration of components away from the main stream. Fractions are collected at different positions across the bottom of the support.

continuous-flow technique a technique for following rapid chemical reactions in which two solutions, containing the reactants, are rapidly mixed and the mixture pumped at a predetermined speed through a tube of known dimensions that contains an observation chamber. By changing the rate of flow, the time between mixing and observation can be varied. Thus, given a method of analysis for reactants or products in the observation chamber, the extent of reaction as a function of time can be determined.

continuous process a method of cultivation in which nutrients are supplied and components of the culture medium are removed continuously at volumetrically equal rates, maintaining the cells in a condition of stable multiplication and constant growth rate.

continuous variation *or* **Job's method** a method for investigating metal–ligand (or other) equilibria in solution in which the mole ratio of, e.g., metal ion to ligand species is varied while the sum of their concentrations is kept constant and some property that varies in a fashion proportional to the concentration of one of the molecular entities present, e.g. absorbance or conductivity, is measured. The curve of the

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magnitude of the property observed versus the concentration ratio gives information about the stoichiometry of the metal–ligand (or other) complex formed and allows the stability (association) constant to be calculated.

contractile vacuole any of the small spherical vesicles, found in the cytoplasm of freshwater protozoans, that function to expel surplus water from the organism.

contrapsin a glycoprotein plasma serine protease inhibitor, similar to the **serpin**-type inhibitors. It specifically inactivates serine proteases of the trypsin class but not of the chymotrypsin class. It has 64% homology with human α_1-antichymotrypsin. Example (precursor) from *Mus musculus*: database code COTR_MOUSE, 418 amino acids (46.83 kDa).

contributing amino acid (in an enzyme) any amino-acid residue whose only function appears to be that of a foundation for the **contact amino acid** and **auxiliary amino acid** residues in the **active site**. They are required in the natural enzyme to maintain the framework to which the contact and auxiliary amino acids are attached.

contributing structure *or (formerly)* **canonical form** any one of two or more formal valence bond representations of a mesomeric molecular structure. *Compare* **mesomerism**.

control **1** any object or system in an experiment that is a standard of comparison. A control is prepared or carried out exactly as the other parts of an experiment but differs in respect of a single variable, allowing the significance of the latter to be assessed. *Compare* **experimental** (def. 3). **2** the regulation of a biochemical process such as a metabolic pathway or the expression of a gene.

controllability coefficient *former name for* **elasticity coefficient**.

controlled pore glass a type of glass in the form of rigid particles honeycombed with a great number of pores of selected, precisely defined size. It is useful as a supporting matrix in a large variety of chromatographic techniques, including affinity, gel-permeation, and ion-exchange methods.

control point the point – corresponding to a particular enzyme – in a metabolic pathway or other biochemical sequence where control is exercised.

control region *or* **control sequence** the part of a DNA molecule containing the **promoter** and the **operator** region of an **operon**.

control strength *former name for* **flux control coefficient**.

convergence *see* **convergent evolution**.

convergent evolution *or* **convergence** evolution such as to produce an increasing similarity in some characteristic(s) between initially different groups of, e.g., organisms or **gene products**. *Compare* **divergent evolution**.

convertin *an alternative name for* factor VIIa (*see* **blood coagulation**).

convertin enzyme (factor) *see* **serum converting enzyme**.

convolution **1** a twisting together, a coil. **2** a folding, such as those that produce the irregular ridges on the surface of the cerebrum of the brain.

Conway microdiffusion method a microchemical analytical method applicable to substances from which a gas, e.g. ammonia or carbon dioxide, can be liberated quantitatively by a specific reagent or enzyme; the method can also be used to assay an enzyme. The technique employs a special microdiffusion dish, variously termed a **Conway cell**, **Conway dish**, **Conway unit**, or **Conway vessel**. This consists of a shallow circular glass vessel, 40–70 mm in diameter, containing a central well and with a closely fitting lid sealed with grease; the lid closes the outer annular space but does not touch the wall of the central well. The sample is placed in the outer annulus, and a gas-absorbing reagent is placed in the centre well. The specific reagent is added to the sample, the lid is closed, and diffusion of the evolved gas allowed to proceed. Subsequently the remaining gas-absorbing reagent is titrated. [After Edward Joseph Conway (1894–1968), Irish biochemist.]

Coombs's test *an alternative name for* **antiglobulin test**. [After Robert Royston Amos Coombs (1921–), British immunologist.]

cooperative acting together or with others. *See also* **cooperativity**.

cooperative affinity the state of increased potency, receptor affinity, and resistance to destruction that is exhibited by agonist molecules covalently attached to a macromolecule in any situation where ligand and acceptor possess more than one mutual recognition or binding site, deployed in such a manner that simultaneous interaction is stereochemically feasible.

cooperative binding *see* **cooperative ligand binding**.

cooperative feedback inhibition the **feedback inhibition** of an enzyme by two or more end products of a reaction sequence such that the degree of inhibition caused by the mixture is greater than the sum of the effects of the individual end products.

cooperative hydrogen bonding the interaction between adjacent hydrogen bonds in a molecule such that the energy required to form them is less than the sum of the energies required to form the individual bonds, and the energy required to break these bonds is greater than the sum of the energies required to break the individual bonds. Such an interaction increases the stability of the molecular conformation in which it occurs.

cooperative ligand binding the binding of ligands to interacting sites on a macromolecule such that the binding of one ligand molecule to one site either increases (**positive cooperativity**) or decreases (**negative cooperativity**) the affinity of the other site(s) for ligand(s). Such effects may be either **homotropic**, i.e. one ligand species affects the binding of the same ligand species, or **heterotropic** (def. 1), i.e. one ligand species affects the binding of a different ligand species.

cooperativity *(in biochemistry)* any **cooperative** phenomenon, especially **cooperative ligand binding** or the situation in an enzyme that has more than one binding site for its substrate or allosteric effector where the binding of one molecule to the enzyme alters the affinity with which the others are bound.

cooperativity index *see* **saturation ratio**.

coordinate **1** to integrate or classify diverse elements or things. **2** *(in chemistry)* to be or become linked by **coordination** (def. 2). **3** *(in mathematics)* any of a set of values that defines the position of a point in space with reference to a system of axes.

coordinate bond *or* **coordinate covalence** *or* **coordinate link** *an alternative term for* **dipolar bond**.

coordinated enzymes enzymes whose rates of synthesis vary together; they are controlled by cistrons of the same **operon**.

coordinated enzyme synthesis the synthesis of enzymes that are controlled by the genes of one operon and are thus induced or repressed together.

coordinate induction/repression the simultaneous induction/repression of a number of enzymes that catalyse a sequence of either consecutive or related reactions and are controlled by scattered genes.

coordination **1** the balanced and effective interaction of processes. **2** the formation or existence of a covalent bond whose pair of electrons is regarded as originating from only one of the two parts of the molecular entity linked by it; linking by means of such a bond or bonds. *Compare* **colligation**. *See also* **dipolar bond**, **pi adduct**

coordination number *or* **ligancy** the number of other atoms directly linked to a specified atom in a chemical species.

cooxidation *an alternative term for* **co-metabolism**.

COP *abbr. for* coat protein; a protein subunit of a **coatomer**.

copeptin *see* **vasopressin–neurophysin 2–copeptin precursor**.

copigmentation the chemical association between a pigment molecule and another colourless molecule that results in altered absorption characteristics of the pigment and consequently a change in its shade or colour. Some flower petal colours are changed by hydrogen bonding between an anthocyanin pigment and a colourless flavonoid. For example, the anthocyanin in both purple and crimson roses is cyanidin 3,5-diglucoside, but in crimson flowers it is copigmented with

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large amounts of gallotannin. This results in a spectral shift of the absorption maximum by 5 nm to longer wavelengths.

copolymer the product of the polymerization of a mixture of more than one species of **monomer**.

copolymerization *or* **copolymerisation** the polymerization of a mixture of two or more species of **monomer**.

copper-chelate chromatography a type of **metal-chelate affinity chromatography** employing Cu^{2+} ions.

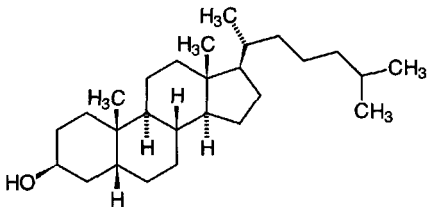
copro+ *or (before a vowel)* **copr+** *comb. form* indicating feces.

coprophagy the act of feeding on feces.

coproporphyrinogen III an intermediate in the biosynthesis of **metalloporphyrins** (hemes and chlorophylls).

coprostane 5β-cholestane; *see* **cholestane**.

coprostanol *or* **coprosterol** 5β-cholestan-3β-ol; a major **sterol** in feces.



copy-choice hypothesis a hypothesis to explain interchromosomal genetic recombination, according to which copying to form a new DNA strand alternates from one parent strand to the other. If the parent strands contain different alleles, a recombinant chromosome may be produced possessing some alleles from one parental strand and some from the other.

copy error a mutation arising from an error in DNA replication.

copy number the number of copies of any gene or plasmid in a given cell. *See* **plasmid**.

CoQ *symbol for* coenzyme Q (obsolete; *see* **ubiquinone**).

$CoQH_2$ *symbol for* reduced coenzyme Q (obsolete; the reduced form of **ubiquinone**).

cord blood blood taken from the umbilical cord.

cord factor 6,6′-dimycolyl trehalose; a highly toxic glycolipid extractable with nonpolar solvents from the cell walls of certain, especially virulent, strains of *Mycobacterium* that characteristically grow in long cords in liquid media.

cordycepin 3′-deoxyadenosine; a substance found in culture fluids of the microfungus *Cordyceps militaris*. It inhibits poly(A) synthesis and interferes with the processing of much eukaryotic mRNA and hence with protein synthesis. The α-^{32}P-labelled 5′-triphosphate is used to label the 3′ ends of DNA fragments in DNA sequence analysis.

cordycepose 3-deoxy-D-ribose; 3-deoxy-D-*erythro*-pentose; the carbohydrate component of **cordycepin**.

core the central, innermost, or least easily destroyed or removed part of a structure; e.g. the core of a partially digested biopolymer, the protoplast core of an endospore, or the core of a virus.

core debranching enzyme *see* **β-1,3-galactosyl-*O*-glycosyl-glycoprotein β-1,6-*N*-acetylglucosaminyltransferase**.

core enzyme the part of bacterial (*Escherichia coli*) **RNA polymerase** lacking the σ subunit. It will catalyse chain elongation but not initiation.

core glycosylation the first of two stages in the biosynthesis of the carbohydrate moiety of some glycoproteins; it takes place in the endoplasmic reticulum.

core particle **1** the RNA-rich particle obtained from a **ribosome** by the gentle removal of some of the ribosomal proteins. The particle retains peptidyltransferase activity. **2** any of the eukaryotic **chromatin** particles containing 140 base pairs of DNA and an octamer of the four conservative **histones** (two each of histones H2A, H2B, H3, and H4) but not histone H1. These particles are obtained by the treatment of chromatin with DNase. In the intact chromatin they are linked by stretches of variable length of so-called linker DNA.

core polymerase *see* **RNA polymerase**.

core protein any of the many types of protein in glycosaminoglycans to which oligosaccharide side-chains are covalently attached and which are themselves covalently attached to a very long oligosaccharide backbone. Each glycosaminoglycan will typically contain many core protein molecules. An example is **heparan sulfate proteoglycan core protein**.

corepressor any metabolite that by its specific combination with a **repressor** causes the activation of the latter.

Cori, Carl Ferdinand (1896–1984) and/or **Gerty Theresa Cori** (née Radnitz, 1896–1957), Czech-born US biochemists distinguished for their studies of glucose and glycogen metabolism, largely carried out in collaboration; joint Nobel Laureates in Physiology or Medicine (1947) 'for their discovery of the course of the catalytic conversion of glycogen' [prize shared with B. A. Houssay].

Cori cycle *or* **lactic acid cycle** an energy-requiring metabolic pathway in animals in which carbon atoms of glucose pass along the circular route: muscle glycogen → blood lactate → blood glucose → muscle glycogen. [After C. F. and G. T. **Cori** who together formulated it in 1929.]

Cori ester *an alternative name for* **α-D-glucopyranose 1-phosphate**. [After C. F. and G. T. **Cori** who reported its isolation in 1936.]

Cori's disease *an alternative name for* type III **glycogen disease**. [After G. T. **Cori** who first described it in 1953.]

cornea the transparent curved part of the front of the eyeball that refracts incident light onto the lens. It is composed of many layers, the thickest being the stroma, which is composed of uniformly fine collagen fibrils. These are kept in an orderly distribution by the expansive force between them of the contained glycosaminoglycan (mainly keratan sulfate I). The cornea has a high oxygen consumption and approximately 50% of the glucose utilized is oxidized via the phosphogluconate pathway. —**corneal** *adj.*

Cornforth (Sir) John Warcup (1917–) Australian-born British organic chemist and biochemist most noted for his elucidation of the stepwise biosynthesis of cholesterol from acetate; Nobel Laureate in Chemistry (1975) 'for his work on the stereochemistry of enzyme-catalyzed reactions' [prize shared with V. **Prelog**].

cornifin *or* **small proline-rich protein I** a cross-linked envelope protein of keratinocytes that first appears in the cell cytosol, but ultimately becomes cross-linked to membrane proteins by transglutaminase. Its presence correlates with squamous differentiation. It is down-regulated by retinoids. Structurally, it is rich in proline, glutamine, and cysteine and contains repeats of an octapeptide, consensus sequence, EPCQPKVP. Example from *Sus scrofa*: database code CORN_PIG, 97 amino acids (10.71 kDa).

corn-steep liquor *or* **corn-steep water** a concentrated fluid obtained by steeping corn (maize) grains in water (containing 0.2% SO_2) for 36–40 hours at 46–50 °C. It is used in the manufacture of **penicillin** to increase antibiotic yield.

corn sugar *a common name for* D-**glucose**.

corn syrup *or (sometimes)* **liquid glucose** a partial hydrolysate of corn (maize) starch containing **glucose** and glucose oligosaccharides.

coronand *an alternative name for* **crown compound**.

coronate *see* **crown compound**.

coronavirus any of a group of RNA animal viruses consisting of enveloped particles 80–120 nm long, with helical nucleocapsids. They include some of the viruses that cause common colds in humans.

corpuscle any living metazoan cell, especially the red corpuscles (erythrocytes) and the white corpuscles (leukocytes) of the blood.

corpuscular radiation *a former term for* **particulate radiation**.

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corpus luteum (*pl.* **corpora lutea**) a yellow, progesterone-secreting, glandular body formed in the mammalian ovary from a **Graafian follicle** after extrusion of an ovum.

correlation *(in statistics)* the interdependence of two or more simultaneously variable quantities; or the nature or degree of this interdependence. If two variates both increase or both decrease together there is said to be **positive (direct) correlation** between them, whereas if they change in opposite directions to each other there is said to be **negative (inverse) correlation**.

correlation coefficient *(in statistics) symbol*: r; a measure of the correlation between two variates, x and y. If one variate has the values $x_1, x_2, \ldots x_n$ and the corresponding values of the other variate are $y_1, y_2, \ldots y_n$, with respective mean values of $\bar{x}$ and $\bar{y}$ then the correlation coefficient, r, is given by:

$$r = \sum_{i=1}^{n}(x_i - \bar{x})(y_i - \bar{y}) \Big/ \left[\sum_{i=1}^{n}(x_i - \bar{x})^2 \sum_{i=1}^{n}(y_i - \bar{y})^2\right]^{1/2}$$

If $r = 0$, x and y are completely independent. If $r = 1$ there is complete correlation and one variate may be calculated from the other variate.

correlation time *symbol*: τ_C; the average time between molecular collisions for molecules in some state of motion. The reciprocal of the correlation time is given by the equation:

$$1/\tau_C = 1/\tau_R + 1/\tau_M + 1/\tau_S$$

where $1/\tau_R$ is the rate at which the molecule is tumbling (τ_R being the **rotational correlation time**), $1/\tau_M$ is the rate at which two dipoles approach each other (τ_M being the **residence time**), and $1/\tau_S$ is the electron spin lattice relaxation rate (τ_S being the time for the upper electron spin state to dissipate its excess energy).

correndonuclease any correctional **endonuclease** that specifically acts on damaged DNA initiating a correctional pathway *in vivo*. The name is misleading because nuclease activity itself does not lead to repair.

corrin $C_{19}H_{22}N_4$, the fundamental heterocyclic skeleton of the **corrinoids**. It consists of four reduced pyrrole rings joined into a macrocyclic ring by links between their α positions; three of these links are formed by a one-carbon unit (methylidyne group) and the other by a direct $C\alpha$–$C\alpha$ bond. Corrin is so named because it is the core of the **vitamin B_{12}** molecule.

corrinoid any of a group of compounds containing the **corrin** skeleton. This group includes various B_{12} vitamins, factors, and derivatives. Some are more unsaturated than corrin itself; many have a regular pattern of substituents on the methylene carbon atoms of the reduced pyrrole rings and a cobalt atom in the centre of the macrocyclic ring.

corrole *a trivial name for* octadehydrocorrin; *see* **corrin**.

cortex (*pl.* **cortices**) **1** the outer layer of an animal organ, situated immediately beneath the capsule or outer membrane. It is usually morphologically distinct from the rest of the organ; e.g. adrenal cortex, cerebral cortex, renal cortex. **2** the unspecialized tissue in plant stems and roots lying between the vascular bundles and the epidermis; the outer layer of a stem. —**cortical** *adj.*

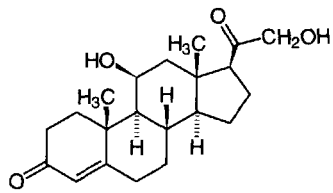
corticoid *an alternative name for* **corticosteroid**.

corticoliberin *an alternative name for* corticotropin-releasing hormone (*see* **CRH**).

corticosteroid *or* **corticoid** any of a large group of C_{21} steroids synthesized from cholesterol in the **adrenal cortex**, especially the adrenocortical hormones. Usage is often extended to include synthetic analogues with hormonal activity. Corticosteroid hormones are divided into **glucocorticoids**, i.e. cortisol and related compounds and **mineralocorticoids**, i.e. aldosterone and related compounds.

corticosteroid-binding globulin *or* **corticosteroid-binding protein** *an alternative name for* **transcortin**.

corticosterone 11β,21-dihydroxypregn-4-ene-3,20-dione; Kendall's compound B; Reichstein's substance H; a **glucocorticoid**, but on the biosynthetic route to aldosterone. Quantitatively it is the second most important corticosteroid of the normal human adrenal cortex. **Cortisol**, synthesized in the adrenal zona fasciculata, is the predominant corticosteroid in humans; corticosterone, synthesized in the adrenal zona fasciculata and glomerulosa, much less so, but it is the main corticosteroid in some rodents.



corticotrope a type of cell in the anterior pituitary that synthesizes **proopiomelanocortin**, a **polyprotein** from which **corticotropin** and a number of other peptide hormones are formed.

corticotrophin *(formerly) a variant spelling of* **corticotropin**.

corticotropin *or* **adrenocorticotropin** *or* **adrenocorticotropic hormone** (*abbr.*: ACTH) a 39-residue polypeptide hormone, secreted by the adenohypophysis of the pituitary, that stimulates growth of the adrenal cortex and the synthesis and secretion of various corticosteroids. It has the sequence (human):

[SYSMEHFRWGKPV]GKKRRPV-
KVYPNGAEDESAEAFPLEF.

The first 13 residues (in brackets) comprise, after proteolysis, **α-melanocyte-stimulating hormone**. Under normal conditions its own secretion is under feedback control from the plasma cortisol level, both directly and through hypothalamic regulatory factors. Biosynthesis occurs via the multihormone precursor peptide **proopiomelanocortin**. Hormonal activity is confined to the species-invariant N-terminal 24 amino acids (*see* **tetracosactide**). Corticotropin secretion is regulated by corticotropin-releasing hormone (**CRH**), is episodic (in bursts at intervals of a few hours), exhibits diurnal rhythm, and is increased by stress such as trauma, surgery, and hypoglycemia. The effects of fever may be mediated by cytokines 1, 2, and 6, which act indirectly by causing the release of CRH. *See also* **corticotropin-like intermediate lobe peptide**, **corticotropin receptor**, **melanotropin**.

corticotropin-induced secreted protein *abbr.*: CISP; *a former name for* thrombospondin-2 (*see* **thrombospondin**).

corticotropin-like intermediate lobe peptide *abbr.*: CLIP; a 22-residue peptide identical in sequence to the C-terminal moiety (residues 18–39) of a molecule of **corticotropin** from the same species. It is obtained from extracts of the pars intermedia of the pituitary of certain animals (rat, pig, dogfish), and has been found also in a carcinoid tumour from a human patient who was secreting ectopic corticotropin; it has not been found in extracts of human pituitary. It is derived from **proopiomelanocortin**. CLIP has B-cell tropin activity and acts to stimulate insulin release from B cells. *See also* **beta-cell tropin**.

corticotropin–lipotropin precursor *see* **proopiomelanocortin**.

corticotropin receptor one of a number of membrane proteins that bind corticotropin and couple to heterotrimeric G-protein-activated **adenylate cyclase**; they are seven-transmembrane-domain proteins and are distributed on cells of the adrenal cortex, on cells of the immune system, and in the brain. EC_{50} values for binding are near 10^{-8} M for corticotropin. Example from *Bos taurus*: database code ACTR_BOVIN, 297 amino acids (33.29 kDa). *See also* **melanocortin receptor**.

corticotropin-releasing factor *an alternative name for* corticotropin-releasing hormone (*see* **CRH**).

corticotropin-releasing-factor binding protein a protein that binds and inactivates corticotropin-releasing hormone (**CRH**), to prevent inappropriate pituitary-adrenal stimulation in pregnancy. Example (precursor) from human: database code CRFB_HUMAN, 322 amino acids (36.15 kDa).

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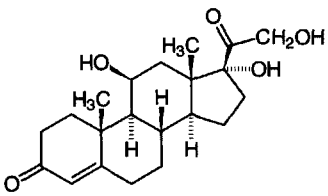
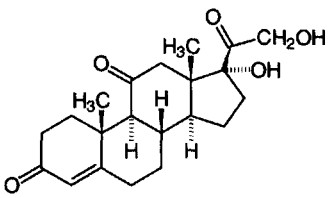
corticotropin-releasing hormone *see* **CRH**.

cortisol *or (recommended name)* **hydrocortisone** 17-hydroxycorticosterone; 11β,17,21-trihydroxy-4-pregnene-3,20-dione; Kendall's compound F; Reichstein's substance M; the most powerful naturally occurring **glucocorticoid** hormone and the most abundant product of the adrenal cortex in humans. It is produced by the cells of the zona reticularis; its best known action is anti-inflammatory. The biosynthesis of cortisol is under the control of **corticotropin**.



cortisol-binding globulin *or* **cortisol-binding protein** *abbr.*: CBG; *an alternative name for* **transcortin**.

cortisone 11-dehydrocortisol; Kendall's compound E; Reichstein's substance F; a prodrug that is biologically inactive but is converted in the liver and, to a lesser extent, in other tissues, to cortisol, a substance with **glucocorticoid** activity. Cortisone was the first glucocorticoid to be isolated and made available for therapeutic use. It is not a primary secretory product of the adrenal cortex, being formed during tissue metabolism from cortisol by 11β-hydroxysteroid dehydrogenase. In fetal plasma, however, cortisone levels are about three times higher than those of cortisol.



cortoic acid any member of a group of acidic metabolites of 17-hydroxycorticosteroids in which the primary alcohol group at C-21 has been oxidized to a carboxylic-acid group. They are the principal acidic metabolites of **cortisol** in humans.

corynecin any of a number of antibiotic compounds produced by the cultivation of *Corynebacterium* KY 4339 in a medium containing C_{12} to C_{14} alkanes as the sole carbon source. Their antibacterial properties are similar to those of **chloramphenicol** but they are less potent.

coryneform **1** club-shaped. **2** describing any Gram-positive, asporogenous, club- or rod-shaped bacterium belonging to the genera *Corynebacterium* or *Brevibacterium*, possibly related to *Streptomyces*. Such bacteria are of biotechnological importance (amino-acid fermentations) and are amenable to genetic manipulation. **3** any coryneform microorganism.

cos *abbr for* **cosine**.

COS cell any member of a cell line, derived from monkey cells, that contains an integrated segment of **SV40** DNA coding for T antigen. Hence these cells will support replication of vector molecules containing the SV40 origin of replication, but no other DNA sequences from that virus.

cosec *abbr. for* cosecant.

cosecant *abbr.*: cosec *or* csc; the reciprocal of the **sine** of an angle.

cosine *abbr.*: cos; a trigonometric function defined, for a given angle of a right-angled triangle, as the ratio of the length of the side adjacent to the angle and the length of the hypotenuse. The cosine of an obtuse angle is numerically equivalent to that of its supplement but of opposite sign.

cosmid a hybrid **cloning vector** used for cloning DNA. Cosmids are derived from plasmids but also contain ***cos* sites** from phage lambda.

***cos* site** the cohesive ends (sticky ends) of certain **phage** DNA molecules. The *cos* site usually referred to is from phage lambda.

costamere a vinculin-containing myofibril attachment site. Costameres form one of the major linkage sites of the skeletal muscle cell, encircling the cell and connecting the Z-discs to the sarcolemma.

co-stimulator *an alternative name for* **interleukin 2**.

cost-selectivity equation a relation between the accuracy gained by editing and the cost in terms of the wasteful hydrolysis of correct products in any enzyme system synthesizing informational macromolecules. It is useful in the rationalization of some observations and proposed editing mechanisms.

cosubstrate an imprecise term used for an organic cofactor that is necessary for the activity of some enzymes. Although not the substrate of principal interest, the cosubstrate acts as an acceptor or donor of atoms or of functional groups and participates stoichiometrically in the reaction. *Compare* **coenzyme**.

COSY *abbr. for* correlated spectroscopy; a technique employed in the first two-dimensional **NMR** experiment, designed to elucidate which resonances of the NMR spectrum are connected by spin–spin J-coupling. J-couplings arise out of the perturbation of the nuclear energy levels of one nuclear spin by another nuclear spin that is propagated through the intervening electronic orbitals. In a one-dimensional NMR spectrum these J-couplings are manifested as a splitting in the Lorentzian lineshape. In 2D-COSY spectra the couplings are indicated by off-diagonal cross-peaks connecting the frequencies of the J-coupled spectra. Ordinarily the J-couplings are only large enough for pairs of ^1H nuclei separated by a maximum of two or three bonds to exhibit COSY cross-peaks.

Cot *see* C_0t.

cotransduction the **transduction** of two or more identifiable genes in a single event, probably because the transduced element contains more than one genetic locus.

cotranslation *(in recombinant DNA technology)* the synthesis of a hybrid molecule consisting of the desired protein product covalently linked to a normal protein secreted by the organism being used, through translation of a hybrid mRNA molecule generated on the recombinant DNA. —**cotranslate** *vb.*

cotranslational transport the transport of nascent protein chains through the membrane of the cisterna of the endoplasmic reticulum while translation is still proceeding at the ribosome. It is a common phenomenon in higher eukaryotes.

cotransmitter a substance, usually a peptide, that is released from neurons and modifies the actions of the substance regarded as the primary transmitter. For example, vasoactive intestinal peptide is a cotransmitter with acetylcholine, and neuropeptide Y performs a similar role with norepinephrine. Cotransmitters may also have direct effects on target cells.

cotransport the concerted movement of two chemical species across a membrane. *Compare* **antiport**, **symport**.

co-trimoxazole an antibacterial drug that comprises a mixture of **sulfamethoxazole** and **trimethoprim** in a ratio of about 5:1. The combination may have synergistic effects.

Cotton effect an anomalous change in optical rotation with wavelength in the region of an absorption band. As the absorption band is approached there is a change in the rotation to a maximum, which may be either positive or negative, followed by a decrease to a minimum passing through zero at the wavelength of maximum absorption. Similarly there is a change in circular dichroism, either positive or negative, coinciding with the absorption band. The magnitudes and directions of these effects have been used to study macromolecular

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conformations. [After Aimé Cotton (1859–1951), French physicist.]

cotyledon the leaf-forming part of the embryo of seeds. — **cotyledonous** *adj.*

Couette viscometer an instrument for measuring viscosity, consisting of two concentric cylinders separated by a narrow annulus, which is filled with the sample. One cylinder is fixed and the other is rotated. From the angular velocity at a given torque and the dimensions of the cylinders, the viscosity of the sample can be calculated. The Couette viscometer is designed for use at relatively low shear gradients.

coulomb *symbol*: C; the SI derived unit of electric charge; the quantity of electricity transported in one second by a current of one ampere. Hence, 1 C = 1 A s. [After Charles Augustin de Coulomb (1736–1806), French physicist.]

coulomb force *or* **coulombic force** the electrostatic attraction or repulsion between two charged particles. *See* **Coulomb's law**.

Coulomb's law (of electrostatics) the law stating that the force, F, of attraction or repulsion between two point charges, Q_1 and Q_2, is proportional to the product of the charges and inversely proportional to the square of the distance, d, between them multiplied by the permittivity, ε, of the medium between them. Hence, $F = (Q_1Q_2)/\varepsilon d^2$. A similar law exists for magnetism.

coulometer *or* **coulombmeter** *or* **voltameter** an electrolytic cell for measuring a quantity of electricity passing through a circuit containing the cell by determining the amount of a metal (usually copper or silver) deposited on the cathode from a solution of a salt of the metal.

coulometry *or* **coulombmetry** *or* **voltametry** a method of chemical analysis based on the measurement of a quantity of electricity, in coulombs, in an electrode reaction. —**coulometric** *or* **coulombmetric** *adj.*; **coulometrically** *or* **coulombmetrically** *adv.*

Coulter counter a device for counting particles in a suspension, e.g. blood cells, microorganisms, or spores. Its functioning depends on changes in electric conductivity as the particles pass through a small aperture.

coumarin **1** 1,2-benzopyrone; 2*H*-chromen-2-one; a fluorescent indicator. **2** any of a number of coumarin derivatives. The coumarins are important in the perfume industry since they smell of new-mown hay and grass, though some are no longer used (acernocoumarol and phenindiene) because of adverse allergenic effects. Some are useful in forming fluorescent analytes. Others are antibiotics, e.g. **novobiocin** or mycotoxins (*see* **aflatoxin**).

coumarin anticoagulants *see* **dicoumarol**.

counter any device for enumerating, especially one for detecting and determining particles and photons emitted from the disintegration of a radionuclide. *See*, e.g., **Cherenkov counter**, **Geiger counter**, **scintillation counter**.

countercurrent chromatography a form of **partition chromatography** that eliminates the need for a solid support, in which one of the components of a two-phase solvent system is allowed to flow through the second component in a coiled tube. The technique is claimed to have the advantages of both **countercurrent distribution** and **liquid–liquid chromatography** with the disadvantages of neither, and to be applicable to a broad spectrum of samples ranging from micromolecules to macromolecules, particles, and cells.

countercurrent distribution *or* **countercurrent separation** a method for the separation and purification of (usually organic) substances that depends on the repetitive distribution of solute between two immiscible liquid phases in a series of vessels in which the phases are in contact. The process is continued until homogeneous substances are distributed in various sets of vessels in accordance with their **distribution coefficients** between the two liquid phases. *See also* **Craig apparatus**.

countercurrent transport the movement of a solute in or out of a cell against a concentration gradient by an ATP-independent process. It is due to competition between the solute under consideration and a second solute, with an opposite concentration distribution, for the same membrane carrier protein.

counterelectrophoresis *see* **counterimmunoelectrophoresis**.

counterflow the movement of a substance across a membrane against a concentration gradient.

counterimmunoelectrophoresis *or* **counterelectrophoresis** *other names:* countermigration electrophoresis; immunoelectroosmophoresis; *abbr.:* CIE; a one-dimensional double **electroimmunodiffusion**; a technique wherein diffusion of the reactants towards each other, and hence the formation of precipitin lines, is accelerated by the combination of electrophoresis and electroendosmosis that occurs when an electric potential difference is applied across the gel between the antigen- and antibody-containing wells, with the latter positive to the former.

counterion any ion carrying a charge opposite to that of the charged chemical species with which it is associated; an ion of low M_r with a charge of opposite sign to that of the colloidal ion. *Compare* **co-ion**.

countermigration electrophoresis *an alternative name for* **counterimmunoelectrophoresis.**

counterstain **1** to apply a second stain to a preparation for microscopy. Counterstaining is used to stain in a contrasting way those parts of the preparation that have not been stained by the first stain. **2** any stain so used.

countertranscript *an alternative term for* **antisense RNA**.

countertransport *an alternative term for* **antiport**.

countertrypsin a glycoprotein trypsin inhibitor from mouse plasma and a member of the **fetuin** family.

counting efficiency the ratio of recorded radioactivity events to the number of actual radioactive disintegrations occurring in the same time and in the same sample. It is sometimes expressed as the percentage efficiency.

COUP *other names*: COUP-TF; v-ErbA-related protein; EAR-3; a transcription factor named from one activity, chicken ovalbumin upstream promoter. In association with transcription factor IIB it stimulates initiation of transcription. It is similar to the steroid/thyroid/retinoic nuclear hormone receptors and **seven-up**. Example from human: database code COTF_HUMAN, 423 amino acids (46.10 kDa).

couple **1** a pair of equal and opposite, parallel but not collinear, forces acting on a body, thus producing a turning effect. **2** to join or link (two things) together.

coupled assay a type of enzymic assay of a substrate (or of an enzyme) employed when the reaction in question does not give chromophoric or fluorescent products. A second enzyme reaction that acts on one of the products of the first reaction, and that gives an easily detectable product, is carried out simultaneously with the first reaction. Many coupled assays are based on the formation or disappearance of NADH, which can be easily detected by its absorbance at 340 nm.

coupled oxidation and phosphorylation an intimate relationship between oxidation of substrate and phosphorylation of ADP to ATP such that the two processes cannot proceed independently, as in mitochondria. *See also* **coupling** (def. 3).

coupled reaction either of two reactions, one endergonic and the other exergonic, that are linked energetically, occur simultaneously, and share a common intermediate, such that the overall free energy change for the two reactions is negative.

coupling **1** *(in chemistry)* the covalent linking of one chemical entity to another; *see* **covalent bond**. **2** *(in physics)* **a** an interaction between different parts of a system, e.g. between groups of atoms, electrons, or nuclei. **b** an interaction between two electronic circuits so that power is transferred from one to the other. **3** *(in biochemistry)* the linking of **electron transport** and **oxidative phosphorylation** in isolated mitochondria. Thus, if the **phosphorus:oxygen ratio** is high the mitochondria are said to be tightly coupled. *See also* **uncoupling**.

coupling constant the separation between any two bands of multiple peaks in nuclear magnetic resonance spectroscopy; it

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is proportional to the magnitude of the **spin–spin coupling** constant.

coupling factor *abbr.:* CF; *archaic term for* either **1** any of the proteins functioning in the coupling of ATP synthesis to electron transport in mitochondria. CF1–CF4 are obsolete names for the α–δ subunits of mitochondrial **H⁺-transporting ATP synthase**. **2** any of the proteins required for the coupling of ATP synthesis to the photoinduced electron transport in chloroplasts during photosynthesis. The concept has been replaced by the **chemiosmotic coupling hypothesis**.

coupling membrane any biological membrane in which energy-yielding and energy-requiring biochemical processes occur together.

covalence *or* **covalency** nonionic valence between two atoms in a chemical compound, characterized by their sharing of one or more electrons. —**covalent** *adj.*

covalent bond a chemical **bond** formed between two atoms in a molecule by the sharing of electrons, usually in pairs, by the bonded atoms.

covalent catalysis the catalysis of any reaction in which the substrate is modified by forming a covalent bond with the catalyst (enzyme).

covalent chromatography any technique of **column chromatography** in which the substance of interest binds covalently with groups, e.g. –SH groups, on the support medium and is subsequently displaced by an appropriate reagent.

covalent (closed) circle (of DNA) *or* **covalently closed circular DNA** *or* **closed double-stranded DNA** *abbr.:* cccDNA; any double-stranded DNA molecule that is circular (but not necessarily geometrically circular) and in which both polynucleotide strands are completely continuous. *Compare* **Hershey circle**, **open circle**.

covalent modification any of a diverse group of processes in which the initially synthesized structures of biopolymers, especially enzymes, proenzymes, or structural macromolecules, are enzymically modified by the breakage of covalent bonds or the addition of new covalently linked groups. It includes **post-translational modification**. The term may sometimes be used in the more restricted sense of reversible interconversion of active and inactive forms of certain metabolic enzymes or other proteins by sets of control enzymes, often by phosphorylation–dephosphorylation.

covariance a measure of the association between two variables. For n pairs of values of two random variables, x and y, this is given by:

$$\text{Cov.}\,(x,y) = (x - \bar{x})(y - \bar{y})/(n - 1)$$

where $\bar{x}$ and $\bar{y}$ are the means of the populations of x and y, respectively. *Compare* **correlation coefficient**, **regression coefficient**, **variance**.

covarion any of the codons in a given gene that may concomitantly vary, so resulting in favourable mutations or in mutations leading to amino-acid substitutions that have little or no effect. [From concomitantly variable codon.]

covirus any virus that exists as two or more separate particles all of which must be present together in the host organism for the complete replication cycle of the virus to occur.

covolume the amount by which the apparent volume of a molecule exceeds the sum of the volumes of the constituent atoms. It is usually 13–14 $cm^3\ mol^{-1}$ for protein molecules.

cozymase originally, the heat-stable, diffusible fraction of a crude aqueous extract of brewers' yeast that, if added to the heat-labile, nondiffusible fraction (zymase), would enable the alcoholic fermentation of glucose to occur in a cell-free system. The term was subsequently applied to one particular substance present in that fraction, now known as **nicotinamide adenine dinucleotide**.

C_3 pathway *an alternative name for* **reductive pentose phosphate cycle**.

C_4 pathway *an alternative name for* **Hatch–Slack pathway**.

CPBA *abbr. for* competitive protein-binding assay.

CPE *abbr. for* cytopathic effect.

C peptide **1** **a** the inactive polypeptide excised from **proinsulin** during its conversion to insulin. It contains 31 amino-acid residues in the human but shows greater species variability in both length and amino-acid sequence than does insulin. The structure of porcine C-peptide is (including the flanking basic residues):

RREAQNPQAGAVELGGGLGGLQALALEGPPQKR.

It is released into the bloodstream concomitantly with insulin, hence the blood level is useful in evaluation of B-cell function. **b** that segment of the amino-acid sequence of proinsulin lying between the two residues destined to become respectively the C-terminal residue of the B chain of insulin and the N-terminal residue of the A chain. It consists structurally of the above polypeptide plus two flanking pairs of basic residues. C peptide is named from connecting peptide, and perhaps also because, after A (chain) and B (chain), C (peptide) represents alphabetically the third major structural component of proinsulin. **2** *an alternative name for* C fragment (of β-lipotropin) (*see* **lipotronin**).

CpG island a region of 1–2 kb containing a high density of methylated cytosine residues and occurring immediately 5′ to G residues, i.e. in the sequence CpG. CpG islands are frequently found in animal genomes at the 5′ end of genes. In plants the methylated sequence is ...CpNpGp... where N can be any base. Methylation of DNA is a heritable phenomenon that reduces gene expression, probably by increasing the binding of a repressor. CpG islands are a site of high mutational frequency because spontaneous deamination of the methylated cytosine gives thymine, which is not recognized by DNA repair enzymes.

C_3 plant any plant in which fixation of carbon dioxide occurs predominantly by the **reductive pentose phosphate cycle**; i.e. by incorporation initially into the three-carbon compound 3-phosphoglycerate.

C_4 plant any plant in which fixation of carbon dioxide occurs predominantly by the **Hatch–Slack pathway**; i.e. by incorporation initially into the four-carbon compound oxaloacetate. Such plants are found usually in semiarid conditions with high light levels. They include sugar cane, corn (maize), and many weeds.

cpm *or* **c.p.m.** *abbr. for* counts per minute.

Cr *symbol for* chromium.

Crabtree effect the inhibition of respiration by glycolysis. The inhibition is small and occurs only in a few types of cells that possess a high glycolytic capacity, e.g. ascites tumour cells and other neoplastic tissues, renal medulla, leukocytes, and cartilage. *Compare* **Pasteur effect**.

Craig apparatus the most widely used type of apparatus for carrying out **countercurrent distribution** experiments. The earlier version (1944) was constructed of metal and the later version (1949) was of modular design and constructed of glass. [After Lyman Creighton Craig (1906–74).]

crambin a protein obtained from seeds of *Crambe abyssinica*. It comprises 46 amino acids, has a molecular mass of 4.73 kDa (database code CRAM_CRAAB), and is remarkable for its highly ordered crystals and very high resolution. Its 3-D structure is known.

cranin a form of **dystroglycan**.

CRE *abbr. for* cyclic AMP response element; a sequence,

GTGACGT[A/G][A/G],

that is present in many viral and cellular promoters. When it binds **CREB protein**, transcription of the genes regulated by such a promoter is turned on.

C-reactive protein *abbr.:* CRP; an acidic, crystallizable, heat-sensitive protein of ≈118 kDa that is detectable in human or monkey blood serum early in the course of various infections or when there is inflammation, tissue damage, or necrosis. One of the so-called **acute phase proteins**, it is normally un-

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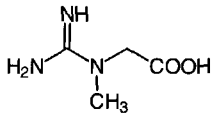
detectable. Not an immunoglobulin and of unknown function, it is named for its ability, in the presence of Ca^{2+} ions, to form a precipitate with a pneumococcal somatic C polysaccharide. Example from human (precursor): database code CRP_HUMAN, 224 amino acids (25.04 kDa).

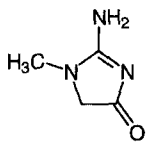
creatine *N*-(aminoiminomethyl)-*N*-methylglycine; an important metabolite in muscle, the precursor of **phosphocreatine**.



creatine kinase EC 2.7.3.2; *systematic name:* ATP:creatine *N*-phosphotransferase; an enzyme that catalyses the formation of **phosphocreatine** from ATP and creatine with release of ADP. The enzyme has M and B subunits, and may exist as the homodimers MM and BB or the heterodimer MB. BB mainly occurs in brain and thyroid, while MM occurs in muscle; MB occurs to a much greater extent in cardiac muscle (30% of total) than skeletal muscle (1% of total) and is thus a useful diagnostic isoenzyme in myocardial infarction, an increased level of the MB isoenzyme occurring between 12 and 36 hours after the infarct. Examples from human; B chain: database code KCRB_HUMAN, 381 amino acids (42.60 kDa); M chain: database code KCRM_HUMAN, 381 amino acids (43.05 kDa); sarcomeric mitochondrial precursor: database code KCRS_HUMAN, 419 amino acids (47.47 kDa); ubiquitous mitochondrial precursor (u-MTCK): database code KCRU_HUMAN, 417 amino acids (46.98 kDa).

creatine phosphate *an alternative name (not recommended) for* **phosphocreatine**.

creatinine 2-amino-1,5-dihydro-1-methyl-4*H*-imidazol-4-one; an end product of creatine metabolism and a normal constituent of urine.



CREB protein *abbr. for* cyclic AMP response element binding protein; a protein that, following phosphorylation by **cyclic AMP-dependent protein kinase** on a single serine residue, binds to the cyclic AMP response element (**CRE**). This then stimulates transcription of genes controlled by regulatory regions that contain the CRE. Example (bovine): database code CREB_BOVIN, 325 amino acids (34.84 kDa).

C region *abbr. for* constant region (of an immunoglobulin).

cretinism a condition of congenital **hypothyroidism** characterized by arrested mental and physical development.

Creutzfeldt–Jakob disease *abbr.*: CJD; a transmissible **spongiform encephalopathy** of humans. It has occurred in three forms: (1) familial (about 15% of cases), (2) iatrogenic or acquired due to inadvertent exposure to CJD-contaminated material, notably human cadaveric growth hormone, and **kuru**, (3) sporadic – the most common form – which is of unknown etiology. They are all associated with the accumulation in affected brains of an abnormal isoform of a glycoprotein. The familial form, which shows an autosomal pattern of disease segregation, is associated with coding mutations in the prion-protein gene. Forms (1) and (3) usually occur in the fifth or sixth decade of life and progress rapidly (within six months) to severe dementia and death typically in one year. Recently a fourth form of CJD has been identified that is believed to be due to consumption of bovine products contaminated with the agent causing **bovine spongiform encephalopathy**. *See also* **prion**. [After Hans Gerhard Creutzfeldt (1885–1964) and Alfons Maria Jakob (1884–1931), German physicians.]

CRF *abbr. for* corticotropin-releasing factor; *see* **CRH**.

CRH *abbr. for* corticotropin-releasing hormone; *other names*: **corticotropin-releasing factor** *or* **corticoliberin** *or* **adrenocorticotropic hormone-releasing factor**; one of a number of peptidic mammalian hypothalamic factors released into the hypophyseal-portal circulation in response to neural and/or chemical stimuli. A 41-residue peptide (M_r 4758.14 human, rat; database code CRF_HUMAN), it controls the secretion by the anterior pituitary gland (i.e. adenohypophysis) of corticotropin, and possibly also of β-lipotropin and pro-γ-melanotropin – all three are peptides formed within the adenohypophysis from proopiomelanocortin. CRH binds to specific seven-transmembrane-domain receptors (e.g. database code CRFR_HUMAN, 444 amino acids (50.72 kDa)) on the **corticotrope** and increases cyclic AMP levels in the cell, stimulating hormone release only in the presence of Ca^{2+}. In addition to increasing the rate of release of corticotropin, it enhances the rate of transcription of mRNA coding for that hormone. *See also* **CRH test**.

CRH test a test that is useful in distinguishing **Cushing's disease** from ectopic corticotropin secretion. If **CRH** is given intravenously, there is an increase in plasma cortisol in normal individuals, while usually in Cushing's disease there is an exaggerated response; in ectopic corticotropin secretion there is usually no cortisol response.

Crick, Francis Harry Compton (1916–), British physicist and molecular biologist famous, *inter alia*, for propounding (with J. D. Watson in 1953) the double-helical structure of DNA, for formulating the adaptor hypothesis of protein synthesis and the central dogma of molecular biology, and for defining the codon; Nobel Laureate in Physiology or Medicine (1962) jointly with J. D. Watson and M. H. F. Wilkins 'for their discoveries concerning the molecular structure of nuclear [*sic*] acid and its significance for information transfer in living material'. *See also* **Franklin**.

Crigler–Najjar syndrome a familial nonhemolytic jaundice and hyperbilirubinemia due to deficiency in hepatic bilirubin glucuronosyltransferase activity. [After John Fielding Crigler (1919–) and Victor Assad Najjar (1914–), US physicians.]

crinophagy a cellular process in which secretion granules fuse with lysosomes. It serves to dispose of excess secretory products in a cell when the stimulus for their discharge is lacking.

crista (*pl.* **cristae**) **1** any of the inward folds of the inner mitochondrial membrane. Their number, extent, and shape differ in mitochondria from different tissues and organisms. They appear to be devices for increasing the surface area of the inner mitochondrial membrane, where the enzymes of electron transport and oxidative phosphorylation are found. Their shape can vary with the respiratory state of the mitochondria. **2** a sensory structure within the ampulla of a semicircular canal of the inner ear.

critical angle *symbol*: C; the least angle of incidence at which total internal reflection of a ray of light or other electromagnetic radiation occurs when passing through a medium and meeting the boundary with a medium of lesser density (e.g. of glass with air).

critical electrolyte concentration *or* **critical salt concentration** the concentration of a particular small ion that will displace an ionic molecule (e.g. of a dye or detergent) of like charge from a polyelectrolyte macromolecule. For example, if a polymer P with z negative charges is stained with a dye R^+, the dyed polymer, $P^{z-}zR^+$, is formed according to the equation:

$$P^{z-}zM^+ + zR^+ \rightleftharpoons P^{z-}zR^+ + zM^+$$

where M^+ is a small cation. Hence the ratio of dyed to undyed polymer, D, is given by:

$$D = [P^{z-}zR^+]/[P^{z-}zM^+] = K[R^+]^z/[M^+]^z$$

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where K is a constant. If z is large, there is a very sharp change in D at a critical value of $[R^+]/[M^+]$. Then if $[R^+]$ is held constant and $[M^+]$ varied, an 'all-or-none' change in D is observed at a well-defined $[M^+]$. This concept is used in the **critical electrolyte concentration method** for staining proteoglycans and polynucleotides, and for fractionation of nucleic acids and other polyanions.

critical micellar concentration *or* **critical micelle concentration** *abbr.*: CMC; *symbol*: c_M; the concentration at which surfactant molecules in a lipid–water mixture begin to aggregate amongst themselves to form micelles in the mixture.

critical pressure the minimum pressure capable of liquefying a gas at its critical temperature.

critical temperature **1** the temperature at or above which a partially miscible two-component system exists as one phase and below which it separates into two phases. **2** the temperature above which liquefaction of a gas cannot occur however great the pressure.

Crk *symbol for* a protooncogene related to v-*crk*, the oncogene of avian sarcoma viruses CT10. The name derives from CT10 regulator of kinase, because the protein causes tyrosine phosphorylation but is not itself a tyrosine kinase. Human Crk contains SH2 and SH3 domains (*see* **SH domain**). Database code: Hscrk, 304 amino acids (33.87 kDa).

CRM *abbr. for* (immunologically) cross-reacting material.

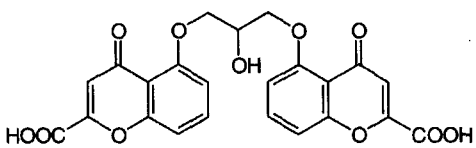
CRM-positive describing a mutant strain of a microorganism that produces a substance that is immunologically cross-reactive with another (specified) substance, e.g. an enzyme or a toxin, produced by a nonmutant (wild-type) strain. Similarly, a **CRM-negative** strain does not produce such a cross-reactive substance.

cRNA *abbr. for* complementary RNA.

cro *symbol for* a regulatory gene in phage lambda, named from 'C-repressor and other things'. Its product, Cro protein, is a repressor that regulates the expression of the *cI* gene. Cro protein is a small globulin, with a **helix-loop-helix** motif; it occurs as a dimer when bound to the operator. Database code RCRO_LAMBD, 66 amino acids (7.36 kDa); 3-D structure known.

Cromer-related blood group a blood group antigen carried by **complement decay accelerating factor**.

cromolyn 1,3-bis(2-carboxychromon-5-yloxy)-2-hydroxypropane; a chromone complex that prevents mast cell degranulation; its mechanism of action is unclear. Commonly prepared as the disodium salt, **disodium chromoglycate**, it is used therapeutically to prevent hypersensitivity reactions, especially asthma.



cross-bridge any connection, seen in electron microcopy, between the contractile elements of muscle, specifically between the head of a myosin molecule and an actin filament.

crossed immunoelectrophoresis *or (sometimes)* **quantitative immunoelectrophoresis** two-dimensional single **electroimmunodiffusion**; a rapid and sensitive technique for separation with high resolution and for quantification of antigenic macromolecules. These are separated first by one-dimensional gel electrophoresis and second by gel electrophoresis orthogonally into a gel containing antibodies to one or more known substances, thereby forming a pattern of loop-shaped precipitation zones between antibodies and corresponding antigens. The height and shape of the loops give information about the quantity and quality of the antigens and of the precipitating antibodies. In **tandem-crossed immunoelectrophoresis** two antigen samples are run at the same time with the application holes placed in such a way that related precipitin peaks formed from the respective samples generate double peaks, permitting direct comparison between them. *Compare* **rocket immunoelectrophoresis**.

crossed immunoisoelectric focusing *or* **crossed immunoelectrofocusing** a two-dimensional separation technique for analysing complex mixtures of macromolecules, e.g. samples of body fluids, that combines the high resolution of **isoelectric focusing** with the selectivity of detection of **immunoelectrophoresis**. Isoelectric focusing in a thin layer of gel (polyacrylamide or, preferably, specially modified agarose) is followed by electrophoresis into an antibody-containing gel orthogonally to the first separation; a pattern of precipitation zones is formed by reaction of antibody with corresponding antigen as in **rocket immunoelectrophoresis**.

crossed-line immunoelectrophoresis a technique that combines the procedures of **crossed immunoelectrophoresis** and **line immunoelectrophoresis**. Antigens are separated in a one-dimensional run (as in crossed immunoelectrophoresis) and the resulting gel is applied to the edge of a spacer gel in which a strip of gel containing a uniform mixture of the antigens (as used in line immunoelectrophoresis) is embedded parallel to the edge; this combination of the spacer gel and the first gel is then applied to the edge of an antibody-containing gel into which the antigens are introduced by electrophoresis. The resulting sum pattern of crossed immunoelectrophoresis peaks, each standing on individual baselines, permits a direct comparison of crossed and line immunoelectrophoresis patterns and in addition provides a higher power of resolution.

cross-flow filtration a method of operating a filtration device in which retained fluid is circulated over the membrane surface thus preventing undue build up of filtered material on the membrane.

cross-hybridization *or* ***cross-hybridisation*** *the hybridization* of a polynucleotide probe to another polynucleotide molecule.

crossing over the reciprocal exchange of segments at corresponding positions along pairs of homologous chromosomes by symmetrical breakage and crosswise rejoining of the chromatids. It results in the **recombination** of alleles. In eukaryotes, crossing over usually accompanies meiosis. Mitotic homologous recombination, while common in yeast, is rare in higher eukaryotes. *See also* **Holliday junction**.

cross-link a side bond between different chains (or parts of a single chain) of a polymer, increasing molecular rigidity. — **cross-linked** *adj.*; **cross-linking** *n*.

cross-matching a serological procedure used to select blood for transfusion. The donor's erythrocytes are mixed with the recipient's serum; agglutination of the erythrocytes indicates incompatibility, demonstrating that the recipient's serum contains antibodies to the donor's erythrocytes.

cross of isocline the dark cross formed in **flow birefringence** experiments between concentric cylinders when the polarizer and analyser are orthogonal. As the system has cylindrical symmetry, there are two regions where the average orientation is parallel to the polarizer direction and two regions, orthogonal to the first two, where the average orientation is parallel to the analyser. In these regions no light is transmitted and a dark cross appears. *See also* **extinction angle**.

crossover **1** *an alternative term for* **crossover chromatid**. **2** the individual resulting from a **crossing over**.

crossover chromatid a **chromatid** resulting from **crossing over** of corresponding segments of the chromatids of homologous chromosomes.

crossover effect *(in pharmacology)* the phenomenon in which a drug shows a positive effect at one concentration and a deleterious effect at another.

crossover method any method for investigating a metabolic (or electron transport) pathway by application of the **crossover theorem**.

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crossover nuclease a **deoxyribonuclease** that is involved in recombination.

crossover point the point in a series of reactions in a metabolic (or electron transport) pathway, that, when one reaction is specifically inhibited, marks the boundary between reactants whose concentrations increase and reactants whose concentrations decrease. In particular, it is the point in the respiratory chain that, because of the specific action of an inhibitor, marks the boundary between respiratory catalysts that are more reduced and ones that are more oxidized (at steady-state levels). *See also* **crossover theorem**.

crossover theorem a theorem stating that when a series of reactions in a metabolic (or electron transport) pathway is inhibited at a specific reaction, the concentrations of reactants before the inhibited reaction increase above their steady-state values while the concentrations of the reactants after the inhibited reaction decrease below their steady-state values.

crossover unit *an alternative name for* **map unit**.

cross-react to react with a substance other than that for which the reagent is supposedly specific. *Compare* **cross-reaction**. — **cross-reactive** *adj.*

cross-reacting antibody any antibody that is able to react with an antigen that did not specifically stimulate its production. Such cross-reactions may be weaker than the reaction of the antibody with the antigen that caused its production.

cross-reacting antigen **1** any antigen that is able to react with an antibody produced in response to another antigen. This may be because the two antigens share the same determinants or carry determinants that are sufficiently alike stereochemically to enable the antibody to react with both of them. **2** any antigen that has an identical structure in two strains of microorganism, so that antibody raised against one strain will react with the second strain.

cross-reaction the immunological phenomenon in which an antigen reacts with an antibody raised against a different antigen. *See* **cross-reacting antibody**, **cross-reacting antigen**.

cross-reactivation the reappearance of activity in the progeny of a lethal mutant virus following mixed infection of a host cell with one or more active viruses. If the active viruses differ from each other in one or more of their genetic loci, the mutant virus is reactivated by genetic exchange leading to the replacement of its damaged nucleic acid.

cross-sensitivity a state of immunological hypersensitivity to one substance produced by priming an animal with another substance that bears **cross-reacting antigen**.

cross-tolerance **1** a state of immunological **tolerance** to one substance produced by priming an animal with another substance that bears **cross-reacting antigen**. **2** a state of physiological tolerance to one drug resulting from chronic administration of another.

croton oil an oil obtained from the seeds of *Croton tiglinum*, a member of the family Euphorbiaceae. It is an irritant, and contains tumour-promoting **phorbol esters**.

crown compound *or* **coronand** any synthetic macrocyclic polydentate nonplanar (generally uncharged) organic compound a molecule of which has three or more ring heteroatoms (usually nitrogen or oxygen) capable of ligation to a metal ion or other cationic entity. The resulting complex is termed a **coronate**. *See also* **crown ether**. *Compare* **cryptand**.

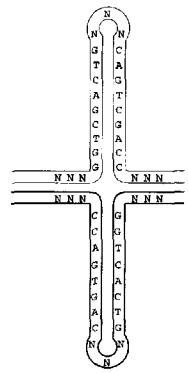
crown ether any of a large subclass of crown compounds that are synthetic macrocyclic polyethers, the molecules of which contain 9–60 atoms in the ring, including 3–20 oxygen atoms. Many crown ethers, especially those containing 5–10 ring oxygen atoms in the molecule, can act as ion-selective complexing agents and ionophores with metal cations; some will solubilize inorganic salts in nonpolar solvents.

crown-gall disease a tumorous disease of many dicotyledonous plants caused by the bacterium *Agrobacterium tumefaciens* and marked by enlargement of the stem near the root crown. The swelling, or **gall**, is produced by the transformation of cells at an infected wound through transfer of the **T-DNA**, part of a large (150–230 kb) plasmid (the **Ti plasmid**) found in oncogenic strains of the bacterium. Transformed tissue is distinguishable by its ability to grow in tissue culture in the absence of plant hormones and by the synthesis of a characteristic **opine**, which is invariably a specific substrate for the particular inducing strain of the bacterium.

CRP *abbr. for* **1** C-reactive protein. **2** cyclic AMP receptor protein; a bacterial **catabolite (gene) activator protein** that complexes with cyclic AMP and binds to specific DNA sites near the promoter to regulate the transcription of several catabolite-sensitive operons. The protein induces a severe bend in DNA and acts as a negative regulator of its own synthesis. It binds to DNA as a dimer. The examples belong to a well-conserved family; there are two motifs. Example from *Escherichia coli*: database code CRP_ECOLI, 210 amino acids (23.61 kDa); 3-D structure of this and many mutants is known. The example from *Shigella flexneri* is identical.

Crt *symbol for* the cerotoyl (i.e. hexacosonyl) group.

cruciform **1** cross-shaped. **2** a DNA conformation that can be generated from long **palindromes**, e.g.



crustacyanin a protein occurring in the carapace of lobsters that binds the carotenoid **astaxanthin**, which provides the blue colour. α-Crustacyanin is a dimer; β-crustacyanin is a 16-mer. There are five types of subunit: A1, A2, A3, C1, and C2; the subunits are **lipocalins**. Example, C1 subunit from European lobster: database code CRC1_HOMGA, 181 amino acids (20.64 kDa).

cruzaine *an alternative name for* **cruzipain**.

cruzipain *or* **cruzaine** a cysteine proteinase (EC 3.4.22.–) that hydrolyses chromogenic peptides at the carboxyl Arg or Lys. It requires at least one more amino acid, preferably Arg, Phe, Val, or Leu, between the terminal Arg or Lys and the amino-blocking group. The purified enzyme digests itself. The enzyme plays a role in development and differentiation of *Trypanosoma cruzi*. Example (precursor): database code CYSP_TRYCR, 467 amino acids (49.78 kDa).

cryo+ *comb. form* indicating low temperature.

cryobiochemistry the study of biochemical substances and processes at subzero temperatures, i.e. below the freezing point of water. The field has expanded because of the development of **cryosolvents**. *See also* **cryoenzymology**.

cryobiology the science that is concerned with the study of the effects of very low temperatures on organisms.

cryoelectron microscopy *see* **electron microscopy**.

cryoenzymology the study of enzymes at low temperatures. By employing temperatures below 0 °C and fluid **cryosolvents**, enzyme reaction rates can be reduced sufficiently for normally transient enzyme–substrate intermediates to be studied.

cryogen any substance used to produce a low temperature; e.g. a freezing mixture.

cryogenic of, or relating to, very low temperatures.

cryogenics the branch of science concerned with the production of very low temperatures and the study of phenomena occurring at these temperatures.

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cryoglobulin any **globulin**, especially IgG or IgM, that forms a gel or flocculent precipitate, or spontaneously crystallizes, on cooling of a solution or a sample of serum containing it. *See also* **cold-insoluble globulin**.

cryomicrotome any **microtome** arranged in a **cryostat** and used to prepare thin sections of frozen tissue for microscopic examination.

cryoprecipitate the precipitate of a **cryoglobulin**.

cryopreservation the science of preserving cells, tissues, or organs over long periods with the aid of very low temperatures.

cryoscope any instrument or device for the determination of freezing points.

cryoscopy the measurement of freezing points, especially the determination of relative molecular mass or osmotic pressure by measurements of freezing point depressions. —**cryoscopic** *adj.*

cryosolvent any mixture of water and one of a select number of polar organic solvents that is used to maintain proteins in fluid solution at temperatures below 0 °C without denaturation.

cryostat an apparatus used to produce and maintain a constant low temperature in an enclosure or liquid bath.

cryosublimation the process whereby water, or another solvent, is sublimed from a frozen sample and is collected in a cold trap. *Compare* **lyophilization**.

cryotolerant tolerant of low temperatures.

cryptand any synthetic macrooligocyclic organic compound, a molecule of which consists of two or more rings linked together by bridgehead (generally nitrogen) atoms to form a three-dimensional cagelike molecular structure having sufficient space within it to accommodate any one of various cations and thereby form a **cryptate**. *Compare* **crown compound**.

cryptate the adduct of a **cryptand** and a metal ion or other cationic entity. The cation is bound within the molecule by polydentate ligation to heteroatoms in the cryptand, an exceptionally stable compound being formed.

cryptic **1** hidden, secret. **2** not apparent, unrecognized, masked; e.g. of a medical condition. **3** (especially of the colouring of an animal) serving to conceal. **4** of a particle-bound enzyme, that it is not as accessible to substrate as when it has been solubilized.

crypticity *or* **latency** the property of being **cryptic**.

cryptic plasmid a **plasmid** to which no phenotypic traits have been ascribed.

crypto+ *or (before a vowel)* **crypt+** *comb. form* meaning secret, hidden, concealed, unrecognized.

cryptotope a hidden immunological determinant. *Compare* **epitope**.

cryst. *abbr. for* crystalline, or crystallized.

crystal any three-dimensional solid aggregate in which the plane faces intersect at definite angles and in which there is a regular internal structure of the constituent chemical species.

crystal lattice the array of **unit cells** along parallel straight lines that makes up the structure of a crystal.

crystallin any of numerous water-soluble structural proteins found in the lens of the eye. Together the crystallins account for almost 90% of the total lenticular protein. Most vertebrate lenses contain three major classes of crystallins, designated α-, β-, and γ-; in birds and reptiles there is a fourth, designated δ-. ε-Crystallin is homologous with the enzyme **lactate dehydrogenase**. Although there are wide variations between species in the proportions of the various crystallins and in the extent of their post-translational modification or degree of aggregation, they display noteworthy conservation of primary structures. Examples from golden hamster: α-crystallin A chain, database code CRA2_MESAU, 196 amino acids (22.50 kDa); B chain, database code CRAB_MESAU, 175 amino acids (20.07 kDa).

crystalline *abbr.:* cryst.; having the structure or characteristics of a **crystal**; made up of crystals; like a crystal.

crystallize *or* **crystallise** to form, or cause to form, crystals, e.g. by slowly removing solvent from a solution to make a solute form one or more crystals.

crystallized *or* **crystallised** *abbr.:* crys.; (of a substance) having been induced into a crystalline form.

crystallography the study of the geometric forms of crystals. *See also* **X-ray crystallography**. —**crystallographer** *n.*; **crystallographic** *adj.*

crystalloid **1** *an alternative term for* **crystalline**. **2** any solute that can pass through a semipermeable membrane that does not allow the passage of a **colloid**. **3** any of the protein crystals that occur in seeds and other plant storage organs.

Cs *symbol for* cesium.

CS *abbr. for* choriomammotropin.

CSD *abbr. for* cold-shock domain (*see* **cold-shock protein**).

CSF *abbr. for* **1** cerebrospinal fluid. **2** colony stimulating factor.

CSP *abbr. for* cell surface protein; *see* **fibronectin**.

CSPCP *abbr. for* cartilage-specific proteoglycan core.

C_ot *or* **Cot** a measure of DNA kinetic **complexity** used in the renaturation analysis of DNA genomes. It is the product of initial DNA concentration, C_o, and time, t. Highly reiterated sequences will renature at low C_ot values while unique sequences will renature at high C_ot values. $C_ot_{½}$ is the value representing half complete renaturation.

CT *abbr. for* computerized tomography (*see* **tomography**).

CTAB *abbr. for* cetyltrimethylammonium bromide.

CTAP-III *abbr. for* connective-tissue activating peptide III; *see* **LA-PF4**.

CTD kinase *see* **[RNA-polymerase]-subunit kinase**.

ctDNA *see* **DNA**.

C terminus *or* **C terminal** that end of any peptide chain at which the 1-carboxy function of a constituent α-amino acid is not attached in peptide linkage to another amino-acid residue. This function may bear an amide group or other substituent in nonpeptide linkage; more commonly it is free (also unprotonated and negatively charged) – the chain end may then also be termed the **carboxy(l) terminus** or **carboxy(l) terminal**. *Compare* **N terminus**. —**C-terminal** *adj.*

C1-tetrahydrofolate synthase a trifunctional enzyme that consists of two major domains: an N-terminal domain, containing N^5,N^{10}-methylenetetrahydrofolate dehydrogenase and N^5,N^{10}-methenyltetrahydrofolate cyclohydrolase (amino acids 1–304 in the example), and a C-terminal domain containing **formate–tetrahydrofolate ligase** domain (amino acids 305–934). It is a homodimer. Example from human: database code C1TC_HUMAN, 934 amino acids (101.31 kDa).

CTF **1** *abbr. for* CAAT box-binding transcription factor *or* nuclear factor 1 (*abbr.:* NF-I); any of a class of **transcription factors** for the eukaryotic RNA polymerase II promoters, **CAAT box** sequences; CTF binds to DNA as a homodimer. Examples from human: CTF1, database code NFI1_HUMAN, 499 amino acids (54.62 kDa); CTF2, database code NFI2_HUMAN, 430 amino acids (47.85 kDa). **2** *abbr. for* competence transcription factor *or* competence protein K; a product of a bacterial regulatory gene required for expression of late competence genes. Example from *Bacillus subtilis*: database code COMK_BACSU, 192 amino acids (22.43 kDa).

CTGF *abbr. for* connective tissue growth factor.

CTH *abbr. for* ceramide trihexoside (Cer(Hex)$_3$ preferred).

CTP *abbr. for* cytidine 5′-triphosphate.

CTP synthase EC 6.3.4.2; *systematic name:* UTP:ammonia ligase (ADP-forming); *other names:* CTP synthetase; UTP–ammonia ligase. An enzyme responsible for *de novo* synthesis of CTP that in bacteria catalyses the reaction between ATP, UTP, and NH_3 to form CTP, ADP,and orthophosphate. Example from *Escherichia coli*: database code PYRG_ECOLI, 545 amino acids (60.37 kDa). In animals, the amino group is donated by glutamine. The enzyme bears the same EC number and the reaction is analogous to that of the bacterial enzyme, with glutamine replacing ammonium ion, and CTP and glutamate as products. Example from human: database code PYRG_HUMAN, 591 amino acids (66.7 kDa).

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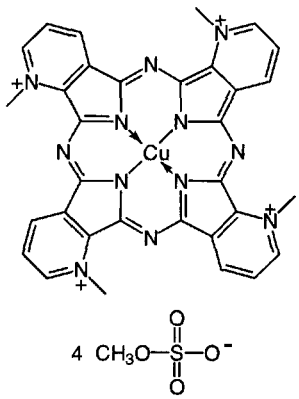
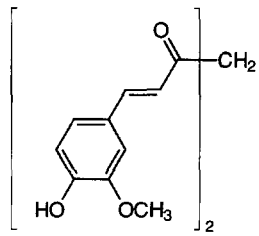
CTS *(in clinical biochemistry) abbr. for* catalase.
Cu *symbol for* copper.
CUA a codon in mRNA for L-leucine.
cubic symmetry the symmetry of one of the three **point groups** of a globular oligomeric protein; it may be **tetrahedral**, designated T_n, where n is 12; **octahedral**, designated O_n, where n is 24; or **icosahedral**, with 60 identical subunits.
CUC a codon in mRNA for L-leucine.
cucurbitacin any of a group of complex triterpenoids that are the bitter principles of the cucumber family, Cucurbitaceae.
CUG a codon in mRNA for L-leucine.
culture **1** (**a**) a collection of cells, tissue fragments, or an organ that is growing or being kept alive in or on a nutrient medium (i.e. **culture medium**); *see also* **cell culture, tissue culture**. (**b**) any culture medium to which such living material has been added, whether or not it is still alive. **2** the practice or process of making, growing, or maintaining such a culture. **3** to grow, maintain, or produce a culture.
culture medium any nutrient medium that is designed to support the growth or maintenance of a **culture** (def. 1). Culture media are typically prepared artificially and designed for a specific type of cell, tissue, or organ. They usually consist of a soft gel (so-called solid or semisolid medium) or a liquid, but occasionally they are rigid solids.
cUMP *abbr. for* cyclic UMP; *see* **uridine 3′,5′-phosphate**.
cumulative inhibition the inhibition of an enzyme resulting from the action of a number of **effectors**, each of which reduces the activity of the enzyme by a fixed percentage irrespective of the degree of inhibition already extant as a result of the presence of other inhibitors.
cuprein any of a group of copper proteins now known as **superoxide dismutase**.
Cuprolinic Blue *the proprietary name for* quinolinic phthalocyanine (*abbr.:* QPC; no CI number); a new, copper-containing, intensely blue dye used for the visualization of RNA and other polynucleotides. The size and shape of the molecule have been designed to provide an exactly complementary fit between any pair of adjacent isoindole rings in the dye and base pairs in nucleic acids.



cuproprotein any protein containing one or more copper atoms.
curare a poisonous extract from certain tropical South American vines of the genera *Strychnos* and *Chondodendron*, used by Amazon and Orinoco Indians as an arrow poison; it blocks neuromuscular transmission in voluntary muscle and is useful as a muscle relaxant, e.g. in surgery. *See* **(+)-tubocurarine** (the active principle) for the mechanism.
curarize *or* **curarise** to treat with (or as if with) curare; especially to cause muscular relaxation or paralysis. —**curarization** *or* **curarisation** *n.*
curculin a polypeptide present in the fruit of *Curculigo latifolia*, a stimulant herb that grows wild in western Malaysia. It is sweet tasting and has taste-modifying activity. It exists as a homodimer. Database code CURC_CURLA, 114 amino acids (12.37 kDa).
curcumin 1,7-bis(4-hydroxy-3-methoxyphenyl)-1,6-heptadiene-3,5-dione; turmeric yellow; a condiment and dye obtained from dried and powdered rhizomes of *Curcuma domestica (C. longa)*. It provides the characteristic colour of curries, and is also an inhibitor of 5-lipoxygenase and **prostaglandin-endoperoxide synthase** cyclooxygenase activity. *See also* **catechin**.



curdlan *see* **callose**.
curie *abbr.:* Ci *(formerly* C); a non-SI unit of (radio)activity or of radioactive material. Originally (1910) it was defined as the quantity of radon in radioactive equilibrium with one gram of radium. Latterly (1968) it was defined as a unit of activity equal to 3.7×10^{10} disintegrations per second or, less correctly, as the quantity of any radioactive material having such activity. Hence, 1 Ci = 3.7×10^{10} **becquerels**. [After Pierre **Curie** (not after Marie Curie as sometimes stated).]
Curie **1 Marie Curie** (née Marie Sklodowska, 1867–1934), Polish-born French chemist and physicist, co-discoverer of radium with her husband, P. Curie (*see* def. 2); Nobel Laureate in Physics (1903) jointly with P. Curie 'in recognition of the extraordinary services they have rendered by their joint researches on the radiation phenomena discovered by Professor Henri Becquerel' [prize shared with A. H. Becquerel]; Nobel Laureate in Chemistry (1911) ' in recognition of her services to the advancement of chemistry by the discovery of the elements radium and polonium, by the isolation of radium and the study of the nature and compounds of this remarkable element'. **2 Pierre Curie** (1859–1906), French physicist and chemist, co-discoverer of radium with his wife, M. Curie (*see* def. 1); Nobel Laureate in Physics (1903) jointly with M. Curie. *See also* **Joliot–Curie**.
curing *(in genetics)* the elimination of a **plasmid** from its host cell.
curtain electrophoresis *see* **continuous-flow electrophoresis**.
cushingoid of, or relating to, **Cushing's disease** or **Cushing's syndrome**, or any of the signs and symptoms associated with these conditions.
Cushing's disease a pituitary-dependent, corticotropin-induced, bilateral adrenal hyperplasia which is one of several conditions embraced by **Cushing's syndrome**. [After Harvey Williams Cushing (1869–1939), US neurosurgeon.]
Cushing's syndrome the group of symptoms and signs resulting from prolonged exposure to inappropriately high plasma **cortisol** concentrations, caused either by primary disease (e.g. tumour) of the adrenal glands or by excessive production of **corticotropin** because of disease (e.g. basophil tumour) of the anterior pituitary. It may also be caused by excessive secretion of cortisol or corticotropin from ectopic sites, or by prolonged therapy with (large doses of) cortisol or other glucocorticoids. The syndrome is characterized by obesity of the trunk, polycythemia, osteoporosis, and glycosuria. The underlying disorder may be corticotropin-dependent or -independent. Of the corticotropin-dependent disorders, **Cushing's disease** is the

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most common, accounting for 68% of all types of Cushing's syndrome. The remainder (15% of all types) result from ectopic corticotropin-secreting tumours, that is, non-endocrine tumours such as lung, gut, ovarian, or carcinoid, which in some cases secrete corticotropin. Corticotropin-independent disorders include adrenocortical adenoma (5%) or carcinoma (3%) and nodular adrenal hyperplasia (9%).

cut **1** to sever, to make an incision, to divide (with a sharp instrument). **2** to separate into **fractions**. **3** a double-stranded scission in a polynucleotide duplex. *Compare* **nick**. **4** informal term for a **fraction**, such as one obtained in column chromatography or distillation.

cutaneous of, pertaining to, or in the skin.

cutinase an enzyme that catalyses the hydrolysis of the plant polyester, cutin, to allow penetration by phytopathogenic fungi. Example from *Asochyta rabiei*: database code CUTI_ASCRA, 223 amino acids (23.49 kDa); five motifs.

CUU a codon in mRNA for L-leucine.

cuvette a small transparent vessel, often with parallel sides of specified separation, used to hold a liquid specimen, especially for optical or spectral measurements. *See also* **cell** (def. 2).

C-value the quantity of DNA present in a single haploid genome.

Cya *symbol for* a residue of the α-amino acid cysteic acid (an artefact in peptide sequences).

cyan+ *a variant form (before a vowel) of* **cyano+**.

cyanate **1** the anion, $N{\equiv}C{-}O^-$, derived from cyanic acid ($HOC{\equiv}N$). **2** any salt of cyanic acid. **3** any organic compound containing the monovalent group $-O-C{\equiv}N$. *Compare* **isocyanate**.

cyanelle a cyanobacterium-like structure, considered as a descendant of an ingested cyanobacterium, that exists as an endosymbiont in the biflagellate protist *Cyanophora paradoxa*. The cyanelle has photosynthetic properties resembling those of cyanobacteria but its genome size is about 10% of those reported for cyanobacteria.

cyanhydrin *a former name for* **cyanohydrin**.

cyanide **1** the anion, $N{\equiv}C^-$, derived from hydrocyanic acid (HCN). This ion blocks the electron transport chain by reacting with the ferric form of cytochrome aa_3 and thus acts as an inhibitor of respiration. **2** any salt of hydrocyanic acid. **3** any organic compound containing the monovalent cyano group, $-C{\equiv}N$; such a compound may also be known either as a nitrile or as a carbonitrile, depending respectively on whether its carbon atom is included in or excluded from the numbering of an attached chain.

cyanide-resistant respiration a respiratory pathway, occurring only in plant mitochondria, that is unaffected by **cyanide**. Electron transport from NADH or succinate to O_2 involves a nonheme iron protein as the terminal oxidase; this is insensitive to cyanide. The cyanide-resistant pathway complements the more usual cyanide-sensitive pathway; this contains cytochrome oxidase, which is inhibited by cyanide. Cyanide-resistant respiration is not found in animals.

cyano+ *or (before a vowel)* **cyan+** *comb. form* denoting **1** the cyanide ion or hydrocyanic acid. **2** the –CN group in covalent linkage. **3** (dark) blue.

cyanobacteria *or (formerly)* **blue-green algae** a very heterogeneous group of prokaryotic photosynthetic organisms all of which contain chlorophyll *a*, carotenoids, and phycobiliproteins arranged in thylakoids. They lack chloroplasts, unlike true algae, and differ from photosynthetic bacteria, in, e.g., evolving oxygen during photosynthesis. Many can fix nitrogen.

cyanoborohydride any member of a group of compounds with the structure MBH_3CN, where M is an alkali metal (usually sodium). They are reducing agents similar in action to borohydride but more stable, more lipophilic, and more selective. They are especially useful for the facile reduction of aldehydes and ketones in acid conditions to the corresponding alcohols, for the reductive amination of aldehydes and ketones in the presence of an amine, and for the reductive methylation of amines (including amino acids and proteins) in the presence of formaldehyde.

cyanocobalamin the most usual form of **vitamin B_{12}**, in which the sixth position on the cobalt atom in **cobalamin** is filled by a cyanide group (the cyanide group being an artefact of the isolation procedure).

cyanogen bromide *or* **bromine cyanide** CBrN, or CNBr, or BrCN; a volatile solid (at ordinary temperatures) with two main uses in biochemistry: (1) in the sequencing of proteins, because (in 90% formic acid) it converts methionine residues in peptide linkage to homoserine residues, with simultaneous cleavage of peptide bonds whose carbonyls are contributed by methionine residues; also (in anhydrous heptafluorobutyric acid) it specifically cleaves tryptophanyl peptide bonds; and (2) for activating cross-linked agarose so that almost any molecule containing amino groups can be coupled to it to prepare a specific affinity adsorbent.

cyanogenesis the production or yielding of cyanide ions or hydrocyanic acid.

cyanogenic *or* **cyanogenetic** **1** *or* **cyanophoric** describing any glucoside or other glycoside containing a cyano group that is released as hydrocyanic acid on acid hydrolysis; e.g. amygdalin. Such compounds occur in the kernels of various fruits. **2** describing any plant that synthesizes such a glycoside.

cyanoginosin a cyclic heptapeptide toxic agent responsible for numerous cases of poisoning among South African livestock that consume water contaminated with blooms of cyanobacteria. About seven variants are known.

cyanoglobin an unusual monomeric myoglobin-like hemoprotein found in multicellular cyanobacteria. Example from *Nostoc commune*: database code GLBN_NOSCO, 118 amino acids (12.89 kDa).

cyanohydrin *or (formerly)* **cyanhydrin** any member of a class of α-hydroxynitriles formed by the base-catalysed addition of a cyanide ion to an aldehyde; such compounds are formed also from some reactive ketones.

cyanolabe a pigment sensitive to blue light (445 nm) that is found in some cones of the retina in the eye. It is lacking in subjects with blue-blindness. *Compare* **chlorolabe**, **erythrolabe**.

cyanophage any virus whose host is a cyanobacterium.

cyanophoric *an alternative term for* **cyanogenic** (def. 1).

cyanophycin granule *or* **structured granule** a type of granule, without apparent limiting membrane, that is observed in most, if not all, cyanobacteria. These granules are variable in size and shape, with diameters up to about 500 nm, and contain polypeptides of 25–100 kDa with a 1:1 arginine:aspartic acid ratio. They are believed to act as a nitrogen reserve.

cyanopsin a greenish-blue, light-sensitive, visual pigment occurring in the cone cells of the retinas of freshwater and migratory fishes and some amphibians. It consists of a cone-type opsin combined (as a Schiff's base) with 3,4-didehydro-11-*cis*-retinal. It has an absorption maximum at about 620 nm, and is analogous in function to **iodopsin** in other vertebrates. *See also* **3,4-didehydroretinal**.

cyanosis the bluish appearance of the skin and mucous membranes due to insufficient oxygenation of the blood in the capillaries. —**cyanotic** *adj.*

cyanosome *an alternative name for* a **phycobilisome** in cyanophytes.

cybrid a portmanteau word used to denote a line of cultured mammalian cells that is a cytoplasmic hybrid of two other lines, as shown by inheritance of biochemical or other characteristics.

cycacin methylazoxymethanol β-D-glucoside; a toxic substance from the seeds of *Cycas revoluta*, the aglycon of which is carcinogenic.

cycl+ *a variant form (before a vowel) of* **cyclo+**.

cyclamate the anion of cyclamic acid, cyclohexylsulfamic acid. It is used in some countries as a sweetening agent, but is banned in the USA because of its possible carcinogenicity.

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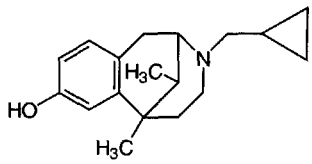
cyclase any enzyme that catalyses ring closure, e.g. **adenylate cyclase**.

cyclazocine 3-(cyclopropylmethyl)-1,2,3,4,5,6-hexahydro-6,11-dimethyl-2,6-methano-3-benzazocin-8-ol; a potent benzomorphan narcotic analgesic agent. It is an antagonist at μ-, and an agonist at δ- and especially κ-opioid receptors. Binding to σ-receptors may explain its psychotomimetic actions.



cycle **1** any recurring period of time in which certain events or operations occur, complete themselves, or repeat themselves in a regular sequence. **2** any sequence of changes occurring in a system in which the system is eventually restored to its initial state. **3** *(in biochemistry)* any closed sequence of metabolic reactions in which an end product acts as a reactant in the initiation of the cycle, e.g. the **tricarboxylic-acid cycle**. **4** *(in ecology)* any closed sequence of large-scale processes that describes the nutritional interdependence of animals, plants, and microorganisms, e.g. the **nitrogen cycle**. **5** to process through a cycle or cyclic system; to pass through cycles or to vary in a cyclical manner.

cyclic **1** of, relating to, moving in, or being a cycle. **2** (of an organic chemical compound) containing one (i.e. monocyclic) or more (i.e. polycyclic) rings of atoms. *Compare* **heterocyclic**, **homocyclic**. —**cyclically** *adv.*

cyclic adenosine 5′-diphosphoribose *or* **cyclic ADP-ribose** *abbr.:* cyclic ADPR *or* cADPR; a metabolite derived from NAD^+ and thought to be responsible for mediating certain of the latter's regulatory effects. It consists of a ribose molecule linked by its C-5 hydroxyl to the β-phosphate of ADP and by its C-1 hydroxyl to the adenosine amino group. It is suggested that it is involved in regulating intracellular Ca^{2+} concentrations and in activating the nonskeletal form of the ryanodine receptor Ca^{2+} channel.

cyclical *a variant form of* **cyclic** (def. 1).

cyclic AMP *or* **cAMP** *abbr. for* adenosine 3′,5′-phosphate. *See also* **adenylate cyclase**.

cyclic AMP-dependent protein kinase a **protein kinase** that is regulated by cyclic AMP (cAMP). There are two types with respect to regulation. In **type I**, the inactive form of the enzyme is composed of two regulatory chains and two catalytic chains; activation by cAMP produces two active catalytic monomers and a regulatory dimer that binds four cAMP molecules. Expression of regulatory chains varies among tissues and is in some cases constitutive and in others inducible. Example (human): database codes: KAP0_HUMAN (α regulatory chain), 381 amino acids (42.93 kDa); KAP1_HUMAN (β regulatory chain), 379 amino acids (43.03 kDa). In **type II**, regulatory chains mediate membrane association by binding to anchoring proteins, including the **MAP-2** kinase and **AKAP**. The inactive form of the enzyme is composed of two regulatory chains and two catalytic chains; activation by cAMP produces two active catalytic monomers and a regulatory dimer that binds four cAMP molecules. Database codes: KAP2_HUMAN (α regulatory chain), 417 amino acids (46.16 kDa); KAP3_HUMAN (β regulatory chain), 403 amino acids (45.34 kDa); catalytic subunits (α, β, γ respectively): database codes KAPA_HUMAN, 350 amino acids (40.41 kDa); KAPB_HUMAN, 350 amino acids (40.44 kDa); KAPG_HUMAN, 350 amino acids (40.24 kDa).

cyclic AMP phosphodiesterase (number EC 3.1.4.17 shared with **cyclic GMP phosphodiesterase**); *recommended name*: 3′,5′-cyclic-nucleotide phosphodiesterase; an enzyme that catalyses the hydrolysis of a nucleoside 3′,5′-cyclic phosphate to a nucleoside 5′-phosphate. The intracellular concentration of cyclic AMP is regulated by low-affinity (type 1) and high-affinity (type 2) enzymes. Examples (yeast) type 1: database code CNA1_YEAST, 369 amino acids (42.00 kDa); type 2: database code CNA2_YEAST, 526 amino acids (60.83 kDa). The enzymes are monomers; type 2 is well conserved.

cyclic AMP receptor any of various receptor molecules that bind cyclic AMP, especially **CRP** (def. 2), a bacterial catabolite (gene) activator protein. Other examples are the signalling receptors of the slime mould, *Dictyostelium discoideum*, which are similar to other eukaryotic G-protein-linked receptors. Receptor 1 is involved in aggregation, and receptor 2 is expressed after aggregation in pre-stalk cells. Receptor 1: database code CAR1_DICDI, 392 amino acids (44.26 kDa); receptor 2: database code CAR2_DICDI, 375 amino acids (43.26 kDa).

cyclic AMP response element *see* **CRE**.

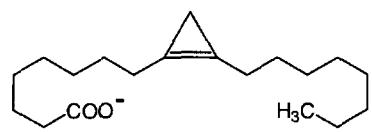
cyclic analysis a procedure that is useful, e.g. in flame spectrophotometry, for minimizing the effects of any mutual interference between two or more components of a sample being analysed. First, the concentration of each such component is estimated. Next, standards for each of the components are prepared containing the other interfering components at their estimated concentrations and the estimations are repeated. Then fresh standards are prepared, using the revised values for the concentrations of the interfering components, and further estimations are made; and so on, until a constant and accurate value for each component is obtained. In practice, usually only two or three such cycles of analysis are necessary.

cyclic CMP *see* **cytidine phosphate**.

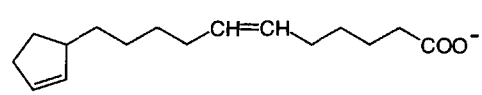
cyclic diguanylic acid bis(3′-5′)cyclic guanylic acid; a potent activator of cellulose synthase in the bacterium *Acetobacter xylinum*.

cyclic electron flow *see* **cyclic photophosphorylation**.

cyclic fatty acid any of a class of fatty acids that contain a carbocyclic unit. They include those with a cyclopropane unit, such as **lactobacillic acid** found in bacterial membranes, those with a cyclopropene unit such as sterculic acid (*see* structure), found in Sterculiaceae, and those with a cyclopentene unit, found in seed fats of Flacourtiaceae, these including manaoic acid (*see* structure). **Mycolic acids** are 2-alkyl-3-hydroxy acids with up to 80 carbons, and contain cyclopropane units. Fatty acids containing a cyclohexane unit are also known.



sterulic acid



manoic acid

cyclic GMP *abbr. for* guanosine 3′,5′-phosphate.

cyclic GMP phosphodiesterase (EC 3.1.4.17, number shared with **cyclic AMP phosphodiesterase**); *recommended name*: 3′,5′-cyclic-nucleotide phosphodiesterase. An enzyme that catalyses the hydrolysis of a nucleoside 3′,5′-cyclic phosphate

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to a nucleoside 5′-phosphate. It is involved in the regulation of the concentration of cyclic GMP, and thereby involved in the transmission and amplification of the visual signal; *see* **guanosine 3′,5′-phosphate**. Example from mouse rod cells has three subunits: α and β are catalytic subunits (short form of β is β′ from alternative splicing), and γ is a regulatory subunit; α and β are typical cyclic nucleotide phosphodiesterases. α database code CNRA_MOUSE, 858 amino acids (99.40 kDa); β database code CNRB_MOUSE, 856 amino acids (98.39 kDa); γ database code CNRG_MOUSE, 87 amino acids (9.63 kDa).

cyclic IMP *symbol:* cIMP *or* Ino-3′,5′-*P*; inosine 3′,5′-(cyclic)phosphate.

cyclic nucleotide any nucleotide in which the phosphate group is in diester linkage to two positions on the sugar residue, usually 3′,5′ but also sometimes 2′,3′.

cyclic photophosphorylation the processes that occurs in photosystem I in which the high-potential electron in bound ferredoxin can be transferred to cytochrome b_{563}, rather than to $NADP^+$, and then back to the oxidized form of P700 through cytochrome c_{552} and plastocyanin with the generation of one molecule of ATP. *See* **photosystem**.

cyclic symmetry the symmetry of a **point group**, designated C_n, having a geometric arrangement of the subunits such that a rotation of 360°/*n* transposes the structure into itself (i.e. it is indistinguishable from the original one). A dimeric molecule with chemically and spatially identical subunits must necessarily belong to the point group C_2. In general, a molecule with C_n symmetry will be a closed ring containing *n* subunits (e.g. of triangular, square, pentagonal, and hexagonal appearance for molecules containing three, four, five, and six subunits, respectively). If *n* is an odd number, C_n is the only symmetry possible.

cyclic UMP *symbol:* cUMP *or* Urd-3′,5′-*P*; uridine 3′,5′-(cyclic)phosphate.

cyclin any of a group of proteins that are involved in regulation of the eukaryotic **cell-division cycle**. Cyclins periodically rise and fall in concentration in step with the cycle. Individual cyclins activate particular **cyclin-dependent protein kinases** and thereby help to control progression from one stage of the cycle to the next (e.g. $p34^{cdc2}$/cyclin B regulates the G_2 to M transition in all eukaryotes). All the following examples are from *Saccharomyces cerevisiae*: (1) G_1/S-specific cyclin Cln1; this is essential for control of the cell cycle at the G_1/S (START) transition; it interacts with the Cdc28 protein kinase to form S-phase promoting factor (**SPF**); database code CG11_YEAST, 546 amino acids, (62.11 kDa). (2) G_1/S-specific cyclin Cln2; this has an overlapping function with Cln1. Cln1 and Cln2 mRNAs fluctuate in the cell cycle; database code CG12_YEAST, 545 amino acids (61.62 kDa). (3) G_2/mitotic-specific cyclin C1B1; this interacts with the Cdc2 protein kinase to form MPF. G_2/M cyclins accumulate steadily during G_2 and are abruptly destroyed at mitosis; database code CG21_YEAST, 471 amino acids (54.81 kDa). G_2/mitotic-specific cyclins C1B2–4 are similar. (4) S-phase entry cyclins C1B5 and 6; these are maximally expressed just before the S-phase of the cell cycle; database code CGS5_YEAST, 435 amino acids (50.37 kDa). *See also* ***cdc* gene**, **cyclin-dependent protein kinase**, **cyclin regulatory proteins**.

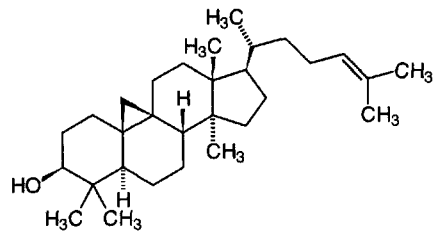
cyclin-dependent protein kinase Cdk; a protein kinase that is only active when complexed with a regulatory protein, a **cyclin**. Different Cdk–cyclin complexes are thought to trigger different steps in the cell-division cycle by phosphorylating specific target proteins. *See also* **cyclin regulatory protein**.

cyclin regulatory protein any protein involved in the regulation of **cyclin** gene expression. An example from *Saccharomyces cerevisiae* is Cdc68. This plays a role in general transcription, with both positive and negative effects on gene expression; it is required for the appropriate synthesis during heat shock, and for continued expression of cyclin genes; database code CC68_YEAST, 1035 amino acids (118.50 kDa). A further example, also from yeast, is the Ser/Thr protein kinase Cdc28 (*see* ***cdc* gene**).

cyclitol any cycloalkane containing one hydroxyl group on each of three or more ring atoms. Notable members are the **inositols** and their derivatives.

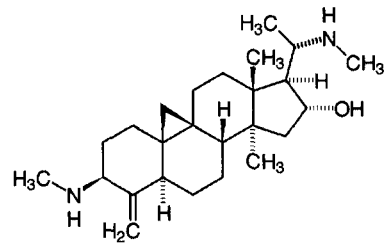
cyclo+ *or (before a vowel)* **cycl+** *comb. form* indicating a circle or ring, especially one in a cyclic organic chemical compound.

cycloartenol the first triterpene intermediate in the biosynthesis of sterols in photosynthetic tissues. It is formed from (*S*)-squalene-2,3-epoxide by a cyclization reaction catalysed by cycloartenol synthase, EC 5.4.99.8. The corresponding intermediate in animal tissues is **lanosterol**.



cyclobutadipyrimidine a type of **pyrimidine dimer** formed within a DNA strand between neighbouring pyrimidine residues.

cyclobuxine a steroidal alkaloid extracted from *Buxus microphylla*. The extracts are used as folk remedies for malaria and venereal diseases. It protects the heart from ischemia and reperfusion damage by inhibiting the release of ATP metabolites during reperfusion.



cyclobuxine D

cyclodeaminase *an informal name for* **formiminotetrahydrofolate** cyclodeaminase.

cyclodepsipeptide *see* **depsipeptide**.

cyclodextrin any of a group of cyclic nonreducing **dextrins** formed from starch or glycogen by the extracellular enzyme cyclomaltodextrin glucanotransferase (EC 2.4.1.19), produced by *Bacillus macerans*. They consist of cyclic polymers containing six, seven, or eight α-(1,4)-linked D-glucose residues. These were formerly known, respectively, as Schardinger α-, β-, or γ-dextrins, or α-, β-, or γ-cyclodextrins, but now are more correctly named cyclomaltohexaose, cyclomaltoheptaose, or cyclomaltooctaose. Cyclodextrins have a toroidal molecular structure enclosing a hydrophobic cavity, thereby permitting the formation of inclusion complexes with a wide variety of molecules.

cyclofenil bis-(*p*-acetoxyphenyl)cyclohexylidenemethane; an agent that prevents feedback inhibition of ovulation by inhibiting the binding of estrogen in the brain. The resulting increased secretion of gonadotropin-releasing hormone, gonadotropins, and estrogen promotes ovulation.

cycloheximide *or* **actidione** 3-[2(3,5-dimethyl-2-oxocyclohexyl)-2-hydroxyethyl]glutarimide; an antibiotic produced by

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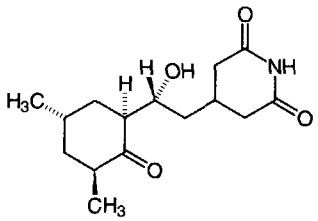
some *Streptomyces* spp. It interferes with protein synthesis in eukaryotes by inhibiting peptidyltransferase activity of the 60S ribosomal subunit.



cyclohydrolase *an informal name for* the enzyme **methenyltetrahydrofolate cyclohydrolase**, EC 3.5.4.9.

cyclo-ligase any **ligase** enzyme of the sub-subclass EC 6.3.3 that catalyses the formation of a heterocyclic ring containing a C–N bond; e.g. dethiobiotin synthase, EC 6.3.3.3.

cyclomaltoheptaose *see* **cyclodextrin**.

cyclomaltohexaose *see* **cyclodextrin**.

cyclomaltooctaose *see* **cyclodextrin**.

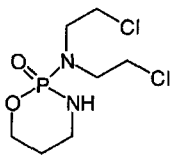
cyclooxygenase *an alternative (informal) name for* **prostaglandin–endoperoxide synthase**.

cyclooxygenation the process that introduces one molecule of dioxygen at C-9 and a second dioxygen at C-15 of a molecule of arachidonic acid, accompanied by formation of a bond between C-8 and C-12 and an endoperoxide bridge across C-9 and C-11.

cyclophilin the protein to which the immunosuppressant **cyclosporin A** binds. Cyclophilin possesses **peptidylprolyl isomerase** activity. The *in vivo* function of this **immunophilin** is not clear.

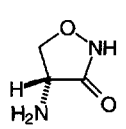
cyclophorase originally, a supposed integrated complex of enzymes that carries out the tricarboxylic-acid cycle, fatty-acid oxidation, oxidative phosphorylation, and terminal electron transport. This system was identified later with **mitochondria**. The cyclophorase complex and the mitochondria are thus the functional and structural sides of the same unit.

cyclophosphamide *N*,*N*-bis(2-chloroethyl)tetrahydro-2*H*-1,3,2-oxazaphosphorin-2-amine 2-oxide; an alkylating agent that is metabolized by the liver cytochrome P450 system to 4-hydroxycyclophosphamide, which is in equilibrium with aldophosphamide. These are transported to tissues, which convert them to the cytotoxic agent, phosphoramine mustard, and acrolein. Cyclophosphamide is useful as an immunosuppressant. *See also* **chlorambucil**.



cyclopropylamine *see* **monoamine oxidase inhibitors**.

D-cycloserine D-4-amino-3-isoxazolidinone; a tuberculostatic antibiotic found in cultures of *Streptomyces orchidaceus*. It is a potent inhibitor of alanine racemase (EC 5.1.1.1) and D-alanine–D-alanine ligase (EC 6.3.2.4; alanylalanine synthetase), two enzymes concerned in the biosynthesis of bacterial cell wall peptidoglycan.



cyclosporin A a cyclic undecapeptide isolated from the fungi *Cylindrocarpon lucidum* and *Tolypocladium inflatum* (formerly *Trichoderma polysporum*). It is a potent immunosuppressive drug that prevents the rejection of allografts, and is used extensively in human transplant operations. Its main target appears to be the T lymphocyte: it contains D-alanine and several nonprotein amino acids, and blocks a calcium-dependent signal from the **T-cell receptor** that normally leads to T-cell activation. When bound to **cyclophilin**, cyclosporin A binds and inactivates the key signalling intermediate **calcineurin**.

cyclotron a machine used to accelerate charged particles of atomic magnitudes to energies of the order of 25 MeV. The particles move in spiral paths under the influence of a uniform vertical magnetic field and are accelerated by a constant frequency electric field.

Cyd *symbol for* a residue of the ribonucleoside **cytidine** (alternative to C).

Cyd*P* *symbol for* cytidine phosphate (*see* **cytidine phosphate**).

Cyd2′*P* *symbol for* cytidine 2′-phosphate (*see* **cytidine phosphate**).

Cyd-2′,3′-*P* *symbol for* cytidine 2′,3′-phosphate (*see* **cytidine phosphate**).

Cyd3′*P* *symbol for* cytidine 3′-phosphate (*see* **cytidine phosphate**).

Cyd-3′,5′-*P* *symbol for* cytidine 3′,5′-phosphate (*see* **cytidine phosphate**).

Cyd5′*P* *symbol for* cytidine 5′-phosphate (*see* **cytidine phosphate**).

Cyd5′*PP* *symbol for* cytidine 5′-diphosphate (*see* **cytidine phosphate**).

Cyd5′*PPP* *symbol for* cytidine 5′-triphosphate (*see* **cytidine phosphate**).

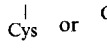
c*-yes** *see* ***YES.

D-cymarose 2,6-dideoxy-3-*O*-methyl-*ribo*-hexose; the D enantiomer is a constituent of some **cardiac glycosides**.

cyproterone 6-chloro-6-dehydro-17α-hydroxy-1,2α-methyleneprogesterone; a progesterone derivative with anti-androgen activity through partial agonist activity at androgen receptors. It inhibits the secretion of gonadotropins and spermatogenesis in humans.

Cyr61 a growth factor binding protein expressed from G_0/G_1 to mid-G_1 of the cell cycle. It is expressed in high amounts in lung. Example (precursor) from *Mus musculus*: database code CYR6_MOUSE, 379 amino acids (41.66 kDa). *Compare* **connective tissue growth factor**.

Cys *symbol for* a residue of the α-amino acid L-cysteine. When written



it represents L-half-cystine.

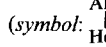
cyst **1** any saclike structure, generally of a pathological nature, comprising a central cavity lined with epithelium and containing fluid or semisolid material. **2** the capsule enclosing a dormant larva or spore. —**cystic** *adj.*

cystamine β,β'-diaminodiethyl disulfide; 2,2′-dithiobis(ethylamine); 2,2′-dithiobisethanamine; $H_2N–CH_2–CH_2–S–S–CH_2–CH_2–NH_2$; the decarboxylation product of cystine and an oxidation product of **cysteamine**.

cystate **1** the **cystine** anion; the dianion, $–OOC–CH(NH_2)–CH_2–S–S–CH_2–CH(NH_2)–COO^–$, derived from cystine. **2** any salt containing the cystine anion. **3** any ester of cystine. *Distinguish from* **cysteate** and **cysteinate**.

***γ*-cystathionase** *see* **cystathionine *γ*-lyase**.

cystathionine *trivial name for* *S*-(β-amino-β-carboxyethyl)-homocysteine; (*R**)-2-amino-4-[(*S**)-2-amino-2-carboxyethylthio]butanoic acid; $HOOC–CH(NH_2)–CH_2–S–CH_2–CH_2–CH(NH_2)–COOH$; a di($\alpha$-amino acid) and a mixed thioether with two chiral centres. L-Cystathionine



(*symbol*: Ala–Hcy), *S*-(L-alanin-3-yl)-L-homocysteine; (*S*)-2-amino-4-[(*R*)-2-amino-2-carboxyethylthio)butanoic acid – in which both moieties are in the L-configuration, does not occur in proteins but is an

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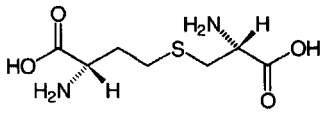
intermediate in the transfer of the sulfur atom from methionine, via homocysteine, to cysteine in mammals. (*Note*: The pair of (*R**,*R**)-enantiomers, in which one moiety is in the D-configuration and the other in the L-configuration, is sometimes known as **allocystathionine**.)



cystathionine γ-lyase EC 4.4.1.1; *systematic name*: L-cystathionine cysteine-lyase (deaminating); *other names*: homoserine deaminase; homoserine dehydratase; γ-cystathionase; cystine desulfhydrase; cysteine desulfhydrase; cystathionase; a multifunctional pyridoxal-phosphate enzyme that catalyses the formation of L-cysteine with release of 2-oxobutanoate and ammonium ion from L-cystathionine and water. It also acts on homoserine and cysteine to remove NH_3, forming oxobutanoate from homoserine or pyruvate and H_2S from cysteine. The enzyme requires pyridoxal-phosphate as coenzyme. Example from human: database code CGL_HUMAN, 361 amino acids (39.49 kDa). It carries out the final reaction in the pathway for the synthesis of cysteine from methionine. Example from *Saccharomyces cerevisiae*: database code CYS3_YEAST, 393 amino acids (42.41 kDa).

cystathionine β-synthase EC 4.2.1.22; *systematic name:* L-serine hydro-lyase (adding homocysteine); *other names:* serine sulfhydrase; β-thionase; methylcysteine synthase. An enzyme that catalyses the reaction between L-serine and L-homocysteine to form cystathionine and water. This is the first step in the synthesis of cysteine from serine. Pyridoxal-phosphate is a cofactor. Example from *Saccharomyces cerevisiae*: database code STR4_YEAST, 507 amino acids (55.96 kDa).

cystathionine γ-synthase EC 4.2.99.9; *recommended name: O*-succinylhomoserine (thiol)-lyase. An enzyme in the pathway for the synthesis of methionine in plants and bacteria. It catalyses the formation of cystathionine from *O*-succinyl-L-homoserine and L-cysteine to form succinate. Pyridoxal-phosphate is a cofactor. The enzyme can utilize hydrogen sulfide or methanethiol as a thiol substrate. Example from *Escherichia coli*: database code METB_ECOLI, 386 amino acids (41.50 kDa).

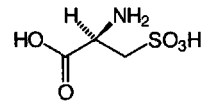
cystathioninuria a condition of humans in which there is excessive excretion of L-cystathionine in the urine. It may be caused by an inherited deficiency of cystathionine γ-lyase.

cystatin any of a group of proteins, present in tissues and body fluids, that inhibit cysteine proteinases. The cystatins constitute a single evolutionary protein superfamily, and are classified into three different families. Family 1 proteins contain about 100 amino-acid residues (M_r 11 000–12 000) and lack disulfide bonds. Family 2 proteins have about 120 residues (M_r 13 000–14 000) with two intrachain disulfide bonds. Family 3 proteins (*also called* **kininogens**) contain three cystatin-like domains, each of which has two disulfide bonds at positions homologous to those in family 2. Examples: cystatin A (*also called* stefin A), database code CYTA_HUMAN, 98 amino acids (10.99 kDa); type 2 cystatin C (*also called* **neuroendocrine basic polypeptide** *or* **post-γ-globulin**): precursor database code CYTC_HUMAN, 146 amino acids (15.78 kDa); this is expressed in highest levels in the epididymis, vas deferens, brain, thymus, and ovary, and is found in sera from patients with Icelandic cerebrovascular type amyloidosis and related diseases.

cysteamine thioethanolamine; β-mercaptoethylamine; 2-aminoethanethiol; $HS–CH_2–CH_2–NH_2$; the decarboxylation product of cysteine. It readily oxidizes in air to **cystamine**. Pantetheine, a component of coenzyme A, is the amide formed between cysteamine and pantothenic acid.

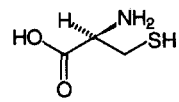
cysteate **1** *the common name for* cysteate(1–); cysteic-acid monoanion; hydrogen cysteate. (*Note:* In theory, the term denotes any ion or mixture of ions formed from **cysteic acid** and having a net charge of minus one, although the species $^-O_3S–CH_2–CH(NH_3^+)–COO^-$ generally predominates in practice.) **2** *the systematic name for* cysteate(2–); cysteate-acid dianion. **3** any salt containing an anion of cysteic acid. **4** any ester of cysteic acid. *Compare* **cystate**, **cysteinate**.

cysteic acid *the trivial name for* 3-sulfoalanine; α-amino-β-sulfopropionic acid; 2-amino-3-sulfopropanoic acid; $HO_3S–CH_2–CH(NH_2)–COOH$; a chiral α-amino acid and an oxidation product of cysteine or cystine. Residues of L-cysteic acid (*symbol*: Cya), (*R*)-2-amino-3-sulfopropanoic acid, do not occur normally in proteins although they are found in wool from the outer part of the fleece of sheep following exposure to sunlight. They are commonly encountered during sequencing of peptides and proteins as the end product of oxidative cleavage of the disulfide bonds of cystine residues and concomitant oxidation of cysteine residues.



cysteinate **1** cysteinate(1–); cysteine monoanion; the anion, $HS–CH_2–CH(NH_2)–COO^-$, derived from **cysteine**. **2** cysteinate(2–); cysteine dianion; the anion, $^-S–CH_2–CH(NH_2)–COO^-$, derived from cysteine. **3** any salt containing an anion of cysteine. **4** any ester of cysteine. *Compare* **cystate**, **cysteate**.

cysteine *the trivial name for* β-mercaptoalanine; α-amino-β-thiolpropionic acid, 2-amino-3-mercaptopropanoic acid; $HS–CH_2–CH(NH_2)–COOH$; a chiral α-amino acid. In neutral or alkaline solution it is readily oxidized by air to **cystine**. L-Cysteine (*symbol*: C *or* Cys), (*R*)-2-amino-3-mercaptopropanoic acid, is a coded amino acid found in peptide linkage in proteins; codon: UGC or UGU. In mammals it is a nonessential dietary amino acid and is glucogenic. D-Cysteine (*symbol*: D-Cys *or* DCys), (*S*)-2-amino-3-mercaptopropanoic acid, occurs naturally in firefly **luciferin**. (*Note*: application of the **sequence rule** to the enantiomers of cysteine results in their stereochemical designation as either *R* or *S* being the converse of that possessed by most chiral α-amino acids found in proteins.)



L-cysteine

cysteine (acid) the protonated form of a **cysteine** residue, i.e. with an undissociated thiol group.

cysteine desulfhydrase *see* **cystathionine γ-lyase**.

cysteine endopeptidase *or (formerly)* **thiol proteinase** any enzyme of the sub-subclass EC 3.4.22, which consists of proteinases characterized by having a cysteine residue at the active centre and by being irreversibly inhibited by sulfhydryl reagents such as iodoacetate. The group includes cathepsins B, H, and L (*see* **cathepsin B**, **cathepsin H**, and **cathepsin L**), **clostripain**, **ficain**, and **papain**. *See also* **apoptosis**.

cysteine-type carboxypeptidase EC 3.4.18.1; *other names*: lysosomal carboxypeptidase B; cathepsin B_2; cathepsin IV;

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acid carboxypeptidase; an enzyme that catalyses the liberation of a C-terminal amino-acid residue from a protein. It is an enzyme with broad specificity, but lacks action on C-terminal proline.

cysteinyl the acyl group, $HS–CH_2–CH(NH_2)–CO–$, derived from **cysteine**. (*Note:* Although this name is formed atypically, its use is recommended to avoid confusion with **cysteyl**.) *Compare* **cystyl**, **half-cystyl**.

cystein-S-yl the alkylthio group, $HOOC–CH(NH_2)–CH_2–S–$, derived from **cysteine**.

cysteyl 1 the acyl group, $HO_3S–CH_2–CH(NH_2)–CO–$, derived from **cysteic acid**. 2 *an alternative name for* **cysteinyl** (use now discouraged).

cystic fibrosis a heterogeneous metabolic disorder affecting all exocrine glands and probably other tissues. It is the most common lethal genetic disorder of Caucasians, although the disease is also found in other races. There is an abnormality in the secretions of the exocrine glands, which have higher than normal concentrations of Na^+, Cl^-, nucleotides, Ca^{2+}, etc.; a number of abnormal protein factors have been described in the exocrine glands of patients. Many cases are due to an abnormality of **cystic fibrosis transmembrane conductance regulator**.

cystic fibrosis transmembrane conductance regulator *abbr.:* CFTR; a 168 kDa integral membrane protein encoded by the cystic fibrosis gene and with a structural similarity to membrane-associated ATP-dependent transporter protein (*see* **ABC transporters**), one of a family of proteins involved in the active transport of ions and small molecules across membranes. CFTR belongs to the **MDR protein** subfamily. The CFTR protein appears to be involved in the functioning of a chloride ion channel. A mutation in this protein has been identified as being responsible for 70% of the cystic fibrosis chromosomes in Northern Europe. Example from human: database code CFTR_HUMAN, 1480 amino acids (167.92 kDa).

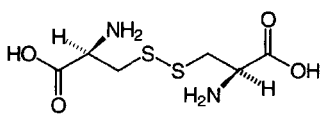
cystine *the trivial name for* dicysteine; β,β′-dithiodialanine; α,α′-diamino-β,β′-dithiobis(propionic acid); (*R**,*R*′*)-3,3′-dithiobis(2-aminopropanoic acid);

$$HOOC–CH(NH_2)–CH_2–S–S–CH_2–CH(NH_2)–COOH;$$

a di(α-amino acid) with two chiral centres, formed by the oxidation of **cysteine**. L-Cystine,

$$[symbol: \overset{\text{Cys}}{\underset{\text{Cys}}{|}}],$$

(*R*,*R*′)-3,3′-dithiobis(2-aminopropanoic acid), is found in peptide linkage in proteins, having been formed by post-translational oxidation of cysteine. In mammals it is a nonessential dietary amino acid and is glucogenic. As it is somewhat insoluble in neutral aqueous solutions, it sometimes forms urinary stones. *meso*-Cystine, (*R*,*S*′)-3,3′-dithiobis(2-aminopropanoic acid), is the internally compensated achiral diastereoisomer, in which D- and L-half-molecules are combined. *See also note* at **cysteine**.



L-cystine

cystine desulfhydrase *see* **cystathionine γ-lyase**.

cystine knot a structure in a protein resulting from three disulfide bonds formed between six cystein residues that are positioned in a way that results in formation of a knot-like topology. It was originally found in transforming growth factor-β and platelet-derived growth factor.

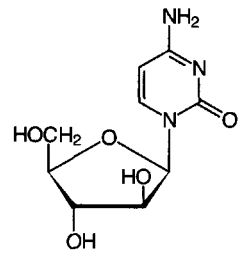
cystinosis a recessively inherited human metabolic disorder characterized by a high intracellular content of free (nonprotein) cystine, apparently compartmentalized within lysosomes, and resulting in deposition of cystine crystals in the cornea, conjunctiva, bone marrow, lymph nodes, leukocytes, and internal organs. —**cystinotic** *adj.*

cystinuria a heritable disorder of cystine and diamino acid (arginine, lysine, and ornithine) transport in humans affecting the epithelial cells of the renal tubules and the gastrointestinal tract. It is characterized by the formation of cystine stones in the urinary tract and elevated levels of cystine and diamino acids in the urine.

cystyl the diacyl group, $–OC–CH(NH_2)–CH_2–S–S–CH_2–CH(NH_2)–CO-$, derived from **cystine**. *Compare* **cysteinyl**, **half-cystyl**.

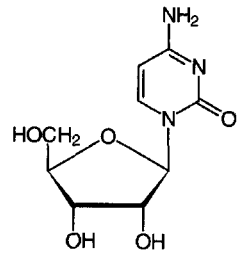
Cyt *symbol for* a residue of the pyrimidine base cytosine (alternative to C).

cytarabine β-cytosine arabinoside; 1-β-D-arabinofuranosylcytosine; *abbr.* ara-C; a cytotoxic drug used as an antineoplastic and antiviral agent. It is effective in the treatment of acute myeloblastic leukemia. It is converted metabolically to 1-β-D-arabinofuranosylcytidine 5′-triphosphate (*abbr.*: *ara*-CTP), a potent inhibitor of DNA synthesis.



+cyte *comb. form* indicating a **cell** (def. 1).

cytidine *symbol*: C *or* Cyd; cytosine riboside; 1-β-D-ribofuranosyl cytosine; a widely distributed **nucleoside**.



cytidine 2′,3′-(cyclic)phosphate *see* **cytidine phosphate**.

cytidine 3′,5′-(cyclic)phosphate *or* **cytidine 3′,5′-cyclophosphate** *see* **cytidine phosphate**.

cytidine deaminase EC 3.5.4.5; *systematic name:* cytidine aminohydrolase. An enzyme that catalyses the reaction:

$$\text{cytidine} + H_2O = \text{uridine} + NH_3.$$

It is a homodimer, with bound Zn^{2+}. Specificity is poor, and deoxycytidine is also a substrate. Example from *Escherichia coli*: database code CDD_ECOLI, 294 amino acids (31.50 kDa).

cytidine 5′-diphosphate *symbol*: Cyd5′*PP or* ppC; *the recommended name for* cytidine diphosphate (*abbr.*: CDP), 5′-diphosphocytidine, 5′-cytidylyl phosphate, cytidine 5′-(trihydrogen diphosphate), a universally distributed nucleotide that occurs both in the free state and as a component of certain **nucleotide coenzymes**. It is a metabolic precursor of cytidine 5′-triphosphate, CTP. It is a product of nucleoside

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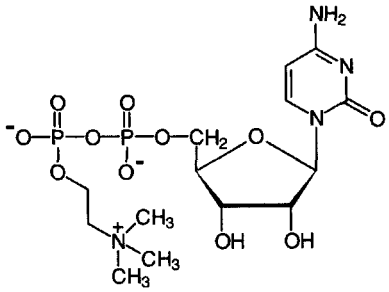
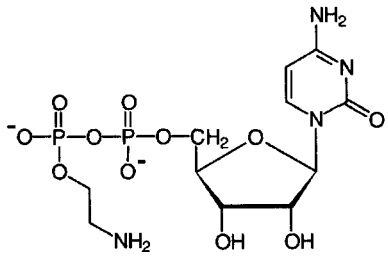
triphosphatase, EC 3.6.1.15, and is also formed in a few cases when CTP is involved in phosphotransferase reactions (e.g. dolichol kinase, EC 2.7.1.108); it is converted to deoxycytidine 5′-diphosphate by **ribonucleoside-diphosphate reductase** (EC 1.17.4.1).

cytidine(5′)diphosphocholine *or* **cytidine diphosphate choline**; intermediate in phospholipid synthesis, especially of phosphatidylcholines and sphingomyelins.



cytidine(5′)diphosphoethanolamine *or* **cytidine diphosphate ethanolamine**; intermediate in the synthesis of phosphatidylethanolamines.



cytidine monophosphate *abbr.*: CMP; an alternative name for any cytidine phosphate, but in particular for cytidine 5′-phosphate, especially when its distinction from cytidine (5′-)-diphosphate and cytidine (5′-)triphosphate requires emphasis.

cytidine phosphate *symbol*: Cyd*P*; cytidine monophosphate (*abbr.*: CMP); any phosphoric monoester or diester of cytidine. There are three monoesters: cytidine 2′-phosphate, cytidine 3′-phosphate, and **cytidine 5′-phosphate**, and two possible diesters: cytidine 2′,3′-phosphate and cytidine 3′,5′-phosphate, although cytidine 5′-phosphate is the ester commonly denoted (the locant being omitted if no ambiguity may arise). Cytidine 2′,3′-phosphate (*symbol*: Cyd-2′,3′-*P*), also named cytidine 2′,3′-(cyclic)phosphate *or* cyclic cytidine 2′,3′-monophosphate (*abbr.*: 2′,3′-cyclic CMP), is formed as an intermediate during the alkaline hydrolysis of ribonucleic acid. This diester then readily hydrolyses to a mixture of the two monoesters cytidine 2′-phosphate (*symbol*: Cyd2′*P*), *also named* cytidine 2′-monophosphate (*abbr.*: 2′CMP) *or* 2′-cytidylic acid *or* cytidylic acid a, and cytidine 3′-phosphate (*symbol*: Cyd3′*P*), also named cytidine 3′-monophosphate (*abbr.*: 3′CMP) *or* 3′-cytidylic acid *or* cytidylic acid b. Cytidine 3′,5′-phosphate (*symbol*: Cyd-3′,5′-*P*), also named cytidine 3′,5′-(cyclic)phosphate *or* cyclic cytidine 3′,5′-monophosphate (*abbr.*: 3′,5′-cyclic CMP), is a product of cytidylate cyclase, EC 4.6.1.6.

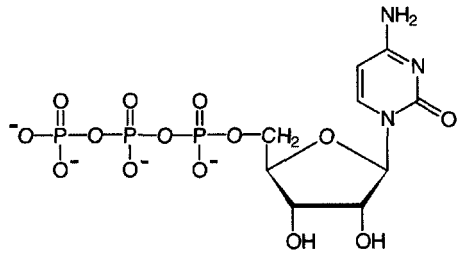
cytidine 2′-phosphate *see* **cytidine phosphate**.

cytidine 2′3′-phosphate *see* **cytidine phosphate**.

cytidine 3′-phosphate *see* **cytidine phosphate**.

cytidine 5′-phosphate *or* **5′-cytidylic acid** *or* **5′-phosphocytidine** *or* **5′-*O*-phosphonocytidine**; *symbol*: Cyd5′*P*; *alternative recommended names for* cytidine 5′-monophosphate (*abbr.*: 5′CMP), cytidine 5′-(dihydrogen phosphate), cytidine (mono)-ribonucleotide. (The locant is commonly omitted if there is no ambiguity as to the position of phosphorylation). It is formed by pyrophosphatase-catalysed cleavage of (inorganic) diphosphate from CTP, and also as a product of a variety of reactions, e.g. that in which phosphatidylcholine is formed from CDPcholine and diacylglycerol (diacylglycerol cholinephosphotransferase, EC 2.7.8.2).

cytidine 5′-triphosphate *symbol*: Cyd5′*PPP or* pppC; *recommended name for* cytidine triphosphate (*abbr.*: CTP), 5′-triphosphocytidine, 5′-cytidylyl diphosphate, cytidine 5′-(tetrahydrogen triphosphate), an important coenzyme. It is formed by **CTP synthase**. It participates as coenzyme in reactions in which a cytidylyl group is transferred e.g. in lipid metabolism, to choline phosphate (EC 2.7.7.15, to form CDP-choline) and similar reactions, or in carbohydrate metabolism to form CDPglucose (EC 2.7.7.33), or in the phosphotransferase dolichol kinase (EC 2.7.1.108).



cytidyl any chemical group formed by the loss of a 2′-, a 3′-, or a 5′-hydroxyl group from the ribose moiety of cytidine. *Compare* **cytidylyl**.

cytidylate **1** either the mono- or the di-(phosphoric) anion of **cytidylic acid**. **2** any mixture of cytidylic acid and its anions. **3** any salt or ester of cytidylic acid.

cytidylic acid *the trivial name for* any phosphoric monoester of cytidine. The position of the phosphoric residue on the ribose moiety of a given ester may be specified by a prefixed locant. *See* **cytidine phosphate**. However, 5′-cytidylic acid is the ester commonly denoted, its locant usually being omitted if no ambiguity may arise. 5′-Cytidylic acid is also an alternative recommended name for **cytidine 5′-phosphate**.

cytidylyl the cytidine[mono]phospho group, the acyl group derived from **cytidylic acid**. *Compare* **cytidyl**.

cytidylylation the process of introducing a cytidylyl group into a substance.

cyto+ *comb. form* indicating a **cell** (def. 1).

cytochalasin any of a group of structurally related fungal metabolites (designated A, B, C, D, E, F, etc.) that share a number of unusual and characteristic effects on cultured mammalian cells. The most notable are inhibition of cytoplasmic cleavage following nuclear division, induction of nuclear extrusion, and inhibition of cell motility. They bind to the growing plus ends of actin filaments, preventing further addition of actin molecules, and thus affect functions that involve assembly and disassembly of actin filaments. The basic structure is a benzyl-substituted hydroisoindolone nucleus to which is fused a small macrolide-like ring. [From Greek *cytos*, cell; *chalasis*, relaxation.]

cytochemical bioassay a technique for the assay of various polypeptide hormones, based on function rather than structure. It involves measuring changes in the biochemical activity of a specific target cell, appropriate to the physiological effect of the hormone in question, by quantitative cytochemical

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methods. It is claimed to be more sensitive and more specific than equivalent radioimmunoassays.

cytochemistry the chemistry of living cells, especially the cellular localization of biochemical substances and processes; microscopical biochemistry. —**cytochemical** *adj.*

cytochrome any member of a class of hemoproteins whose characteristic mode of action involves the transfer of electrons in association with a reversible change in oxidation state (between Fe(II) and Fe(III), and sometimes Fe(IV)) of the heme iron. The name embraces all intracellular hemoproteins except hemoglobin, myoglobin, peroxidases, catalase, tryptophan 2,3-dioxygenase, nitrite and sulfite reductases, and heme-thiolate proteins. There are four major established subclasses; well-established members of each subclass are generally distinguished by consecutive numerical subscripts; remaining members are designated by a suffixed number based upon the wavelength (in nanometres) of the α-band (e.g. cytochrome c_1, cytochrome c_{555}); *see* **cytochrome absorption bands**. (1) In **cytochromes *a*** the heme prosthetic group contains a formyl side-chain, i.e. heme *a*. (2) **Cytochromes *b*** contain protoheme or a related heme (without a formyl group) as prosthetic group, not covalently bound to the protein. The group includes **cytochrome *o***, **cytochrome P-450**, and **helicorubin**, as well as **ubiquinol-cytochrome *c* reductase**, **cytochrome *b***, **cytochrome b_2**, **cytochrome b_5**, **cytochrome b_{245}**, **cytochrome b_{599}**, **cytochrome b_6**, and **cytochrome b_6–*f*** complex. (3) In **cytochromes *c*** there are covalent linkages, not necessarily thioether linkages, between the heme side-chains and the protein (*see also* **cytochrome *c***, **cytochrome c_1**). (4) **Cytochromes *d*** contain a tetrapyrrollic chelate of iron as prosthetic group, in which the degree of conjugation of double bonds is less than in porphyrin. *See also* **cytochrome *f***.

cytochrome absorption bands three principal absorption bands in the absorption spectrum of many ferrohemoproteins, being the α-band, β-band, and γ-band (*or* **Soret band**), resulting from the absorption of radiation by the heme groups. They are useful in the characterization and study of these proteins. Characteristic absorption maxima for cytochromes *a*, *b*, *c*, and c_1 are for the α-band: 600, 563, 550, and 554 nm respectively; for the β-band: (none for *a*) 532 (*b*), 531 (*c*), and 524 (c_1) nm; and for the γ-band 439, 429, 415, and 418 nm.

cytochrome *b* a component of the eukaryotic mitochondrial **respiratory chain** complex III. It is an integral membrane protein with two hemes, b_{562} and b_{566}. Example (human): database code CYB_HUMAN, 380 amino acids (42.68 kDa).

cytochrome b_2 EC 1.1.2.3; an enzyme (*recommended name*: L-lactate dehydrogenase (cytochrome)) that catalyses the oxidation of L-lactate by 2 ferricytochrome *c* to form pyruvate and 2 ferrocytochrome *c*. Flavin mononucleotide (FMN) and protoheme IX are cofactors. Cytochrome b_2, is a mitochondrial matrix protein induced by lactate during respiratory adaptation (in yeast). Database code CYB2_YEAST (precursor), 591 amino acids (65.46 kDa); the mature enzyme is a homotetramer; 3-D structure is known.

cytochrome b_5 an electron carrier for several oxygenases, present in animal microsomes and in erythrocytes. It is reduced by **cytochrome b_5 reductase**. Two forms are synthesized by alternative splicing. Example (human): database code CYB5_HUMAN, 133 amino acids (15.18 kDa).

cytochrome b_5 reductase EC 1.6.2.2; a flavoprotein (FAD) enzyme that catalyses the reaction:

$$\text{NADH} + 2\ \text{ferricytochrome } b_5 = \text{NAD}^+ + 2\ \text{ferrocytochrome } b_5.$$

cytochrome b_6 *or* **cytochrome b_{563}** closely related to cytochrome *b*, that is part of the *bc* complex functioning between photosystems II and I of photosynthesis. Example (barley, wheat): database code CYB6_WHEAT, 215 amino acids (24.14 kDa).

cytochrome b_6–*f* complex a complex, occurring in chloroplasts, of cytochrome b_6, the 17 kDa polypeptide (*petD* gene product), cytochrome *f*, and the **Rieske protein**.

cytochrome b_{245} a component of the phagocyte oxidase complex. The protein is a dimer (human) of α and β subunits. Examples: α, database code C24A_HUMAN, 194 amino acids (20.80 kDa); β, database code C24B_HUMAN, 569 amino acids (65.13 kDa).

cytochrome b_{599} a cytochrome of photosystem II of photosynthesis. It exists as a dimer of α and β chains. Examples (pea): α chain, database code PSBE_PEA, 82 amino acids (9.27 kDa); β chain, database code (identical in *Oenothera bertiana*), PSBF_PEA, 39 amino acids (4.42 kDa). *See* **photosystem**.

cytochrome *c* a soluble mitochondrial matrix protein that associates with the inner mitochondrial membrane and functions to transfer electrons between **respiratory chain** complexes III and IV. Its structure has been extensively studied and the sequence from many (>60) species determined. Phylogenetic studies show that about 26 residues are completely invariant, especially those with side chains packing against the heme. The apoprotein is nucleus-encoded, synthesized on free ribosomes, and transported into the mitochondrial matrix, for which the action of heme lyase (holocytochrome-*c* synthase) is essential. Example (human and chimpanzee): database code CYTC_HUMAN, 104 amino acids (11.60 kDa).

cytochrome c_1 an inner mitochondrial membrane integral protein that is a component of **respiratory chain** complex III. Comprising 241 amino acids (bovine heart), and with a molecular mass of 27.94 kDa, it transfers electrons directly to cytochrome *c*. Under some conditions it co-purifies with the 'hinge protein' (9.2 kDa) and a small (7.2 kDa) subunit of unknown function.

cytochrome *c* oxidase *or* **cytochrome oxidase** *or* **cytochrome aa_3** EC 1.9.3.1; a copper-containing oxidoreductase enzyme that catalyses the oxidation of cytochrome *c* by dioxygen with the production of water. The reaction is:

$$4\ \text{ferrocytochrome } c + O_2 = 4\ \text{ferricytochrome } c + 2\ H_2O.$$

It is an integral mitochondrial membrane protein comprising a complex of 13 subunits; subunits I, II, and II are encoded in the mitochondrion and the remaining ten are nucleus encoded. Electrons originating in cytochrome *c* are transferred via heme *a* and Cu(a) to the binuclear centre formed by heme a_3 and Cu(b). Subunit I binds the two hemes and Cu(b): database code COX1_HUMAN, 513 amino acids (56.97 kDa). Subunit II binds Cu(a) and cytochrome *c*: database code COX2_HUMAN, 227 amino acids (25.53 kDa).

cytochrome *c* reductase *see* **NADH dehydrogenase**.

cytochrome *f* a cytochrome, designated after the Latin *frons* (leaf), that occurs in high concentration in leaves (up to 25% of the concentration of chlorophyll). It is a typical *c*-type cytochrome, similar to c_1, and is a component of thylakoid membrane, transferring electrons from photosystem II to I. Example, apocytochrome *f* precursor (tobacco): database code CYF_TOBAC, 320 amino acids (35.21 kDa). *See also* **cytochrome b_6**, **cytochrome b_6–*f* complex**.

cytochrome *m* *an alternative name for* **cytochrome P450**.

cytochrome *o* any *b*-type prokaryotic cytochrome containing protoheme as the prosthetic group that, unlike a typical cytochrome *b*, serves as a terminal electron acceptor (cytochrome oxidase) and is autoxidizable by dioxygen. Use of the term is discouraged.

cytochrome P450 *or (sometimes)* **cytochrome *m*** *abbr.*: (of protein) CYP, (of gene) *CYP*; any member of a group of *b*-type cytochromes that are apparently unique in having a sulfur atom ligated to the iron and that, when reduced, form carbon monoxide complexes – the latter are pigments with a major absorption peak (Soret band) near 450 nm hence the name. These cytochromes are enzymes, including unspecific monooxygenase (EC 1.14.14.1), camphor 5-monooxygenase (EC 1.15.15.1), alkane 1-monooxygenase (EC 1.14.15.3), steroid 11β-monooxygenase (EC 1.14.15.4), cholesterol monooxygenase (side-chain-cleaving) (EC 1.14.15.6), prosta-

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cyclin synthase (EC 5.3.99.4), and thromboxane synthase (EC 5.3.99.5). They catalyse the reaction:

$$RH + \text{reduced flavoprotein} + O_2 = ROH + \text{oxidized flavoprotein} + H_2O.$$

They occur in most animal cells and organelles, and in plants and microorganisms, and their chief function is thought to be the monooxygenation of lipophilic substances (RH can be steroid, fatty acid, or xenobiotics), as in the case of cytochrome $P450_{SCC}$, cholesterol monooxygenase (side-chain-cleaving). In mammals, as liver microsomal enzymes, many are inducible by drug and other treatment e.g. the major phenobarbital-inducible cytochrome in rabbit liver microsomes, known as $P450_{LM2}$. The name **heme-thiolate** (or Brit. **haem-thiolate**) **protein** has been proposed on the grounds of a thiolate ligand at the heme being responsible for the group's unusual spectral and catalytic properties.

A classification of this extensive family is being evolved in a new systematic nomenclature. At present, there are 27 families, of which 10 are found in all mammals. Each family consists of a group of proteins that exhibit 40% or greater sequence identity, and the family is described by an Arabic number. Within these families, subgroups of proteins having greater that 55% identity are classified into subfamilies, designated by a capital letter, and individual proteins within subfamilies are arbitrarily assigned numbers. Under this nomenclature, $P450_{LM2}$ is known as CYP2B4, or P4502B4, and the gene as *CYP2B4*. Example, P450 IA1, TCCD inducible, also P450 type 6, P450-C (human): database code CP11_HUMAN, 512 amino acids (58.10 kDa).

cytocuprein *an alternative name for* **superoxide dismutase**.

cytoflav(e) *or* **cytoflavin** *a historical name for* the yellow pigment(s) discovered in heart muscle and other tissues. In some cases these pigments were subsequently shown to be riboflavin or a flavin-containing enzyme, especially **yellow enzyme**.

cytofluorometry a technique for the detection, localization, and estimation of substances in or attached to cells, using naturally fluorescent substances or those to which a fluorescent label has been attached. The technique has many applications, including specific labelling of cells using fluorescent antibodies, using fluorescent **probes** to report intracellular events or membrane dynamics, or following the fate of a protein with a fluorescent label after injection into a cell.

cytogenetics the branch of genetics concerned with correlating inherited traits with cytological features, especially the appearance, structure, and behaviour of chromosomes. —**cytogenetic** *adj.*

Cytohelicase *the proprietary name for* a commercial enzyme preparation consisting predominantly of a 1,3-β-D-glucanase. It is useful for the isolation of protoplasts because it lyses cell walls.

cytokeratin *see* **keratin**.

cytokine any of a varied group of proteins that are released by mammalian cells and have **autocrine** or **paracrine** activity. They elicit from the target cell a variety of responses depending on the cytokine and target cell. Cytokine actions include control of cell proliferation and differentiation, regulation of immune responses, hemopoiesis, and inflammatory responses. Cytokines produced by lymphocytes are known also as **lymphokines**; those produced by monocytes are also called **monokines**. Other types of cytokine include **chemokines**, growth factors, colony stimulating factors, transforming growth factors, interferons, and tumour necrosis factors. *See* **angiogenin**, **colony stimulating factor**, **epidermal growth factor**, **erythropoietin**, **fibroblast growth factor**, **heparin-binding EGF-like growth factor**, **hepatocyte growth factor**, **interferon**, **insulin-like growth factor**, **interleukin**, **leukemia inhibitory factor**, **macrophage inflammatory protein**, **nerve growth factor**, **oncostatin M**, **platelet-derived endothelial growth factor**, **platelet-derived growth factor**, **RANTES**, **stem cell factor**, **transforming growth factor**, **tumour necrosis factor**, **vascular endothelial growth factor**.

cytokine receptor common γ chain a glycoprotein subunit common to the receptors for a variety of interleukins (IL-2, IL-4, IL-7, and IL-13). It is a type I **membrane protein**. Example (precursor) from *Mus musculus*: database code CYRG_MOUSE, 369 amino acids (42.19 kDa).

cytokinesis **1** the changes that occur in the cytoplasm of a cell during nuclear division. **2** the division of the cytoplasm of a parent cell into daughter cells after nuclear division. *Compare* **karyokinesis**.

cytokinin *or* **phytokinin** any of a group of plant hormones that have a stimulatory effect on the division of plant cells and a retarding effect on leaf senescence. They are purine derivatives.

cytolemma *an alternative name for* **cell membrane**.

cytology the branch of science dealing with the origin, structure, function, biochemistry, and life history of cells. It includes the (microscopic) examination of cells, particularly in the detection and diagnosis of disease.

cytolysin any protein, especially an antibody, that can induce **cytolysis**.

cytolysis the breakdown of cells, especially by destruction of their outer membranes; the lysis of cells. —**cytolytic** *adj.*

cytometer **1** a **cell counter**. **2** a device for measuring cells.

cytometry the counting and/or measuring of cells in a fluid suspension.

cyton *or* **cytone** the body of a cell, especially a nerve cell, as distinct from its processes.

cytopathic damaging to cells.

cytopathic effect the morphological changes that cells may show in response to toxic agents or viruses.

cytopempsis the intracellular phase of **transcytosis**, whereby droplets, molecules, or particles are transported across a polarized cell from one surface to another.

cytophilic having an affinity for cells.

cytophilic antibody any antibody that binds to the surface of cells by means other than by combination of the antibody-combining site with antigenic determinants on the cell surface. Antibody thus fixed to a cell is still able to bind antigens in the vicinity; i.e. the cells become able specifically to absorb antigen.

cytophotometry a technique that employs a combination of microscopy and spectrophotometry for the detection, localization, and determination of substances in cells. It may be done on stained or unstained preparations.

cytoplasm all the **protoplasm** of a living cell excluding the nucleus and the **plasma membrane** but including the other intracellular organelles and structures. Some authors currently also exclude mitochondria, chloroplasts, or other structures containing independently replicating DNA. The term is not synonymous with **cytoplasmic fraction**. *See also* **cytosol**. —**cytoplasmic** *adj.*

cytoplasmic droplet a large (1–8 μm) piece of membrane-bound cytoplasm, containing the usual cytoplasmic organelles (but no nucleus) and one or more large lipid droplets, found in skimmed freshly secreted goat milk. The droplets are capable of triglyceride biosynthesis.

cytoplasmic fraction the material obtained after the removal of unbroken cells, cell debris, and nuclei from a **homogenate** of eukaryotic cells or tissue. It may be further resolved into a **mitochondrial fraction**, a **microsomal fraction**, and a soluble fraction. The term is not synonymous with **cytoplasm**. *See also* **cytosol**.

cytoplasmic gene any extranuclear gene located in certain eukaryotic cellular organelles, e.g. mitochondria and chloroplasts.

cytoplasmic inheritance the inheritance of characters or traits whose determinants are not located on a chromosome. The determinants may be, e.g., viral, mitochondrial, or on plasmids.

cytoplasmic matrix *an alternative name for* **groundplasm**.

cytoplasmic membrane **1** any of the membranous structures

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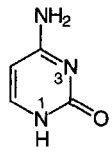
within the **cytoplasm** of eukaryotes, such as the rough and smooth **endoplasmic reticulum** and the **Golgi apparatus**. *See also* **microsomal fraction**, **microsome**. **2** *an alternative term for* **cell membrane** (especially in relation to bacteria).

cytoplast **1** an anuclear eukaryotic cell resulting, e.g., from treatment with cytochalasin B (*see* **cytochalasin**). **2** the apparent single structural and functional unit of the eukaryotic cell, consisting of the **microtrabecular lattice** linking the subcellular organelles and structural fibres.

cytosegresome *an alternative name for* **autophagic vacuole**.

cytosine *symbol:* Cyt; 4-amino-2-hydroxypyrimidine; 4-amino-2(1*H*)-pyrimidinone; a pyrimidine derivative that is one of the five main bases found in nucleic acids; it occurs widely in **cytidine** derivatives.



β-cytosine arabinoside *see* **cytarabine**.

+cytosis *suffix* indicating an increase in the number of cells (in an indicated tissue or organ).

cytoskeleton any of the various filamentous elements within the cytoplasm of eukaryotic cells that remain after treatment of the cells with mild detergent to remove membrane constituents and soluble components of the cytoplasm. The term embraces **intermediate filaments**, **microfilaments**, **microtubules**, and the **microtrabecular lattice**. The various elements of the cytoskeleton not only serve in the maintenance of cellular shape but also have roles in other cellular functions, including cellular movement, cell division, endocytosis, and movement of organelles. (*Note:* The term was coined to describe hypothetical structural cytoplasmic mosaics envisaged as providing physical support for, and thus spatial coordination of, enzymes effecting sequences of reactions, and as imposing restriction of mobility of the cell. Subsequently the cytoskeleton was regarded also as a possible subcellular site of action of various hormones.) —**cytoskeletal** *adj.*

cytosol the part of the **cytoplasm** that does not appear to contain membranous or particulate subcellular components. The term is not synonymous with **soluble fraction**. —**cytosolic** *adj.*

cytosol aminopeptidase *another name for* **leucyl aminopeptidase**.

cytosome any cytoplasmic structure bounded by a single **unit membrane** and of dubious identity.

cytostatic any agent that suppresses cell growth and multiplication.

cytotactin *another name for* **tenascin**.

cytotaxigen any substance that acts indirectly to induce **cytotaxis** by inducing **cytotaxin** formation. For instance, the fixing of complement by antigen–antibody complexes causes the liberation of cytotaxins, and hence cytotaxis. —**cytotaxigenic** *adj.*

cytotaxin *or (sometimes)* **chemotaxin** any chemotactic substance acting directly to induce **cytotaxis**. *See also* **cytotaxigen**.

cytotaxis **1** positive or negative **chemotaxis** of motile cells in response to diffusible substances (cytotaxins) emitted by other cells. **2** the rearrangement of cells leading to the ordering and arranging of new structures. —**cytotactic** *adj.*

cytotoxic causing cell death.

cytotoxicity the attribute of being cytotoxic.

cytotoxicity test any test of cell viability after exposure of cells to (potentially) toxic agents, e.g. antibody and complement. Loss of viability may be demonstrated by a **dye exclusion test**.

cytotoxic T-cell any of a subset of T lymphocytes, bearing the CD8 (human) or Ly2 (mouse) surface marker, that have the ability to kill infected cells. This requires cooperation from T-helper cells. Each cytotoxic T-cell specifically recognizes one antigen, which must be associated with a syngeneic class I MHC molecule.

cytotropism the mutual attraction of two or more cells. —**cytotropic** *adj.*

cytovillin *another name for* **ezrin**.

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Dd

d *symbol for* **1** deci+ (SI prefix denoting 10^{-1} times). **2** a deuteron. **3** day.

d+ **1** *abbr. for* deoxy+ (def. 1); used as a prefix especially to form the symbol dRib for deoxyribose. **2** deoxy+ (def. 2); used as a prefix to form symbols for 2′-deoxyribonucleosides (e.g. dAdo *or* dA for deoxyadenosine) and abbreviations for 2′-deoxyribonucleotides (e.g. dGMP for deoxyguanosine monophosphate).

d *symbol for* **1** diameter, distance, or thickness. **2** relative density.

d- *abbr. for* dextro- used *(formerly) as symbol* denoting dextrorotatory; (+)- should now be used. *See* **optical isomerism**.

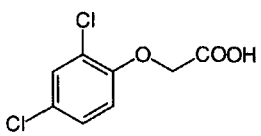
D *symbol for* **1** a residue of the α-amino acid L-aspartic acid. **2** a residue of an incompletely specified base in a nucleic-acid sequence that may be adenine, guanine, or either thymine (in DNA) or uracil (in RNA). **3** a residue of the ribonucleoside (5,6-)dihydrouridine. **4** debye. **5** deuterium (use deprecated).

D600 gallopamil, 5-methoxyverapamil, α-(3-{[2-(3,4-dimethoxyphenyl)ethyl] methylamino}propyl)-3,4,5-trimethoxy-α-(1-methylethyl) benzeneacetonitrile; a drug used in the laboratory to block transport of calcium ions in biological membranes; it is more potent than **verapamil**.

2,4-D *abbr. for* 2,4-dichlorophenoxyacetic acid, a synthetic **auxin** used as a herbicide and to increase latex output from old rubber trees. When sprayed onto foliage at appropriate concentrations it kills broad-leaved plants but not grasses.

D *symbol for* **1** diffusion coefficient. **2** (decadic) attenuance. **3** absorbed dose. **3** (bond) dissociation energy. **4** dilution rate.

***D*$_i$** *symbol for* **1** electric polarization. **2** internal transmission density (*formerly called* optical density).



D- *prefix* denoting one of two possible **absolute configurations** around a chiral element in certain classes of compounds. *See* **D/L convention**.

da *symbol for* deca+ (the SI prefix denoting 10 times).

dA a residue of the deoxynucleoside deoxyadenosine (alternative to dAdo).

Da *symbol for* dalton.

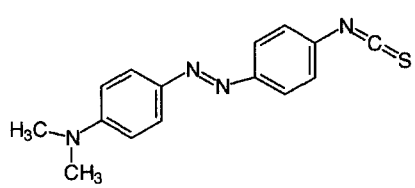
DA *abbr. (sometimes) for* dopamine.

Dab *see* **A$_2$bu**.

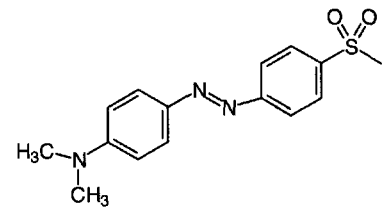
DAB *abbr. for* diaminobutyric acid.

DABA *abbr. for* diaminobenzoic acid.

DABITC *abbr. for* dimethylaminobenzene isothiocyanate, 4-*N*,*N*-dimethylaminoazobenzene 4′-isothiocyanate; a sensitive and versatile chromophoric reagent used in sequencing polypeptides by the **Edman degradation**.



dabsyl *abbr. for* dimethylaminobenzenesulfonyl, 4-dimethylaminobenzene-4′-sulfonyl; a group used as a chromophoric label for free amino groups in amino acids, peptides, and proteins. It is introduced by reaction with dabsyl chloride, 4-dimethylaminobenzene-4′-sulfonyl chloride.



dAdo *symbol for* a residue of the deoxynucleoside deoxyadenosine; 2′-deoxyribosyladenine; adenine 2′-deoxyriboside (alternative to dA).

dAdo5′*P* *symbol. for* deoxyadenosine 5′-phosphate.

DAF *abbr. for* complement decay-accelerating factor.

DAG *abbr. for* diacylglycerol.

DAHP *abbr. for* 3-deoxy-D-*arabino*-(2-)heptulosonate 7-phosphate.

dal *(sometimes) symbol for* dalton (Da is usual).

Dale, (Sir) Henry Hallett (1875–1968), British physiologist and pharmacologist distinguished for his discovery of acetylcholine and for his fundamental physiological studies of the actions of acetylcholine, epinephrine, and histamine (*see also* **Schultz–Dale reaction**); Nobel Laureate in Physiology or Medicine (1936) jointly with O. Loewi 'for their discoveries relating to chemical transmission of nerve impulses'.

Dale's principle the principle that a given neuron is likely to release the same active substance from all its active terminals. Sometimes aggrandized into **Dale's law** – one neuron, one neurotransmitter – its only subsequent modification has been the recognition that a neuron may release more than one active substance. *See* **cotransmitter**.

dalton *symbol*: Da; a non-SI unit of atomic and molecular mass, equal to one-twelfth of the mass of the nuclide carbon-12. It is identical with the **unified atomic mass unit**. It is widely used in biochemistry. Sometimes it is used incorrectly as a supposed unit of the dimensionless terms **relative atomic mass** and **relative molecular mass**. [After John Dalton (1766–1844), British chemist and physicist.]

Dalton's law of partial pressures a statement that the total pressure of a mixture of gases is equal to the sum of the partial pressure of the constituent gases.

Dalziel coefficient any of the coefficients of an equation expressing the initial rate, ν, of a sequential two-substrate enzymic reaction of the form:

$$\nu = EAB / [AB\phi_0 + B\phi_1 + A\phi_2 + \phi_{12}]$$

where E is the enzyme concentration, A and B are the substrate concentrations, and ϕ_0, ϕ_1, ϕ_2, and ϕ_{12} are the Dalziel coefficients. The method can be extended to the evaluation of the eight Dalziel coefficients needed to describe the rate of a three-substrate reaction. [After Keith Dalziel (1921–94), British biochemist.] *Compare* **Michaelis kinetics**.

dam a gene of *Escherichia coli* encoding DNA-adenine methylase. *See* **DNA methylase**.

Dam, Henrik Carl Peter (1895–1976), Danish biochemist noted for his discovery in green plants of an antihemorrhagic principle which he named vitamin K (later termed vitamin K$_1$ or phylloquinone); Nobel Laureate in Physiology or Medicine

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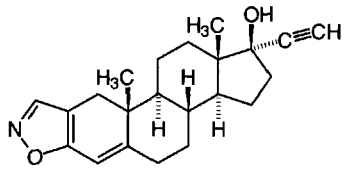
(1943) ' for his discovery of vitamin K' [prize shared with E. A. **Doisy**].

damascenine 3-methoxy-2(methylamino) benzoic acid methyl ester; a **protoalkaloid** from the seeds of *Nigella damascena* (love-in-a-mist) and the odoriferous principle of the oil of nigella.

dAMP *abbr. for* deoxyadenosine monophosphate, the common name for 2′-deoxyadenosine 5′-phosphate; 2′-deoxy-5′-adenylic acid; adenine 2′-deoxyriboside 5′-phosphate.

danazol 17α-pregna-2,4-dien-20-ynol[2,3-*d*]isoxazol-17β-ol; a derivative of ethisterone that is an inhibitor of anterior pituitary function. It inhibits secretion of gonadotropins and synthesis of sex steroids and acts as a ligand for their receptors.



Dane particle *see* **hepatitis**.

Danielli–Davson model *see* **Davson–Danielli model**.

dansyl *symbol*: Dns; *abbr. for* 5-dimethylaminonaphthalene-1-sulfonyl, a group used in **extrinsic fluorescence** studies of proteins. *See also* **dansylate**.

dimethylaminonaphthalene sulfonyl chloride

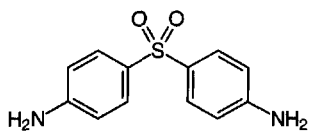
dansylate to derivatize with a dansyl group by reacting with dansyl chloride, 5(dimethylamino)naphth-1-ylsulfonyl chloride. The method is used to acylate free amino groups in protein end-group analysis. The dansyl amino acids, isolated after hydrolysis of the protein, are highly fluorescent and amounts as small as 1 nmol may be detected. —**dansylated** *adj.*; **dansylation** *n.*

Danysz's effect *or* **Danysz's phenomenon** the variation in the toxicity of toxin–antitoxin mixtures dependent on whether toxin is added to equivalence in one lot (nontoxic mixture produced) or in smaller lots over a time period (toxic mixture produced). When added in small lots the toxin reacts with more than one equivalent of antitoxin (antibody) so that insufficient antibody is left to neutralize all the subsequent lots of toxin. [After its discoverer, Jean Danysz (b. 1860), Polish pathologist working in Paris.]

DAP *abbr. for* diaminopimelate.

DAP pathway *see* **diaminopimelic-acid pathway**.

dapsone 4,4′-diaminodiphenyl sulfone; bis(4-aminophenyl)sulfone; an antibacterial and antiprotozoal substance used especially against *Mycobacterium leprae*, the causative agent of leprosy, and as an adjunct in the treatment of malaria. It acts as a competitive antagonist of *p*-aminobenzoic acid and an inhibitor of folate synthesis.



dark adaptation the process by which the rods of the retina gradually become fully responsive to dim light when no longer exposed to bright light. —**dark-adapted** *adj.*

dark band *see* **light band**.

dark current the electric current observed in any photoelectric device in the absence of incident radiation. It is caused by thermal effects.

dark-field microscope *or* **dark-ground microscope** a form of light microscope in which the specimen is illuminated by the apex of a hollow cone of light. On diverging, the light does not enter the aperture of the objective lens, so that unstained or transparent specimens appear as bright objects on a black background.

dark reactions of photosynthesis traditional term for the reactions of the **reductive pentose phosphate cycle** that utilize the ATP and NADPH produced by the light-driven reactions of photosynthesis. The term misleadingly indicates that these reactions occur in the dark. This is true only in the sense that, over very short time intervals, they can occur in the absence of light provided ATP and NADPH are present. However, they are subject to regulatory mechanisms that are stimulated by light, and inhibited by the dark. In growing plants, these reactions occur during daylight hours. The reactions of photosynthesis are used to convert CO_2 into hexoses and other organic compounds by the reactions of the reductive pentose phosphate cycle.

dark reactivation *or* **dark repair** any light-independent enzymic mechanism for the repair of damaged DNA molecules. *Compare* **photoreactivation**.

DATD *abbr. for* diallyltartardiamide, a cross-linking agent.

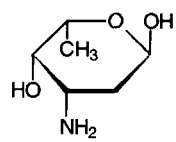
dative bond *an alternative term for* **dipolar bond**.

dATP *abbr. for* deoxyadenosine triphosphate, the common name for 2′-deoxyadenosine 5′-triphosphate, 2′-deoxy-5′-adenylyl diphosphate, adenine 2′-deoxyriboside 5′-triphosphate.

daughter *(as modifier)* **1** denoting a cell (or cell nucleus) produced by the fission of the original (mother) cell or nucleus. **2** denoting either of the two strands of DNA that originate from the parental duplex DNA molecule at replication. **3** denoting a nuclide produced by the nuclear disintegration (either spontaneous or induced) of another nuclide.

daunomycin *or* **daunorubicin** an anthracycline antibiotic and antineoplastic isolated from fermentation broths of *Streptomyces peucetius* widely used in the treatment of cancer. It is a glycoside formed from the tetracyclic aglycon daunomycinone ($C_{21}H_{18}O_8$) and the aminohexose **daunosamine**. It inhibits DNA replication by intercalation into duplex DNA and also inhibits RNA transcription. *Compare* **doxorubicin**.

daunosamine 3-amino-2,3,6-trideoxy-L-*lyxo*-hexose; the aminodeoxy sugar component of **adriamycin**, **daunomycin**, **doxorubicin**, and other antibiotics.



α-L anomer

Dausset, Jean Baptiste Gabriel Joachim (1916–), French physician and hematoimmunologist noted for first establishing the existence in humans of the major histocompatability complex; Nobel Laureate in Physiology or Medicine (1980) jointly with B. Benacerraf and G. D. Snell 'for their discoveries concerning genetically determined structures on the cell surface that regulate immunological reactions'.

Davson–Danielli model *or (sometimes)* **Danielli–Davson**

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model a structural model of the **plasma membrane** consisting, as originally proposed, of a lipid bilayer covered on both surfaces by a film of adsorbed globular proteins. Essentially it was a lamellar model: two sheets of protein separated by a sheet of lipid. The lipid layer had a hydrophobic core and more hydrophilic surfaces. To account for the permeability properties of the plasma membrane the model was subsequently modified by the proposal that pores allow polar solutes to penetrate the lipid layer, and that these pores are lined by protein molecules, providing hydrophilic tubes through the membrane. The model has been totally superseded by more recent concepts. *See* **cell membrane**. [After Hugh Davson (1909–96), British biochemist and physiologist and J. F. Danielli (1911–84), British biochemist.]

day *symbol*: d; a non-SI unit of time equal to 24 hours or 86 400 s.

dbcAMP *abbr. for* dibutyryl cyclic AMP; N^6,$O^{2'}$-dibutyryladenosine 3′,5′-(cyclic)phosphate; a fat-soluble analogue of cyclic AMP, **adenosine 3′,5′-phosphate**.

DBL a gene, isolated and named from a human diffuse B cell lymphoma, that encodes a protein of unknown function and is expressed tissue-specifically in brain, adrenals, and gonads. The protein has been found to catalyse guanine nucleotide exchange *in vitro* on the CDC42Hs protein, a human cell-division-cycle protein. Database code DLB_HUMAN, 925 amino acids (107.66 kDa).

DBM *abbr. for* 2-diazobenzyloxymethyl, $-CH_2-O-CH_2-C_6H_4-N_2^+$; a group that introduces reactive diazonium groups into cellulose or paper forming **DBM-cellulose** or **DBT-paper** in **blot transfer** of proteins or nucleic acids. DBM is formed by diazotization of 2-aminobenzyloxymethyl (ABM) groups previously coupled to the support.

DBMIB *abbr. for* 2,5-dibromo-3-methyl-6-isopropyl-*p*-benzoquinone; a competitor of **plastoquinone** in photosynthetic electron flow.

DBP *see* **vitamin D binding protein**.

d.c. *or* **DC** *abbr. for* **1** direct current. **2** a voltage of constant polarity.

dC *symbol for* a residue of the deoxynucleoside deoxycytidine (alternative to dCyd).

DCC *or* **DCCD** *or* **DCCI** *abbr. for* *N*,*N*′-dicyclohexylcarbodiimide, a coupling agent useful in peptide synthesis and other coupling reactions. *See also* **carbodiimide**.

DCC a human gene, named from 'deleted in colonic carcinoma', that is considered to encode a tumour suppressor, characterized as a cell adhesion molecule of the immunoglobulin superfamily. Database code HSDCCG, 1447 amino acids (158.28 kDa).

D cell *or (formerly)* **A_1 cell** *or* **α_1 cell** a type of endocrine cell of the **apud** series, found in gut mucosa and the pancreatic islets. It was formerly thought to produce gastrin, but is now believed to produce **somatostatin**.

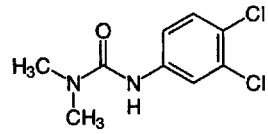
dCMP *or* ***dCyd5′P*** *abbr. for* deoxycytidine monophosphate, the common name for 2′-deoxycytidine 5′-phosphate; 2′-deoxy-5′-cytidylic acid; cytosine 2′-deoxyriboside 5′-phosphate.

dCMP hydroxymethylase *systematic name*: 5,10-methylenetetrahydrofolate:deoxycytidylate 5-hydroxymethyl transferase. EC 2.1.2.8; *other names*: deoxycytidylate hydroxymethylase; deoxycytidylate hydroxymethyltransferase; an enzyme that catalyses the reaction:

5,10-methylenetetrahydrofolate + H_2O + deoxycytidylate = tetrahydrofolate + 5-hydroxymethyldeoxycytidylate.

It is a gene product of T-even bacteriophage; the DNA of these phages contains glycosylated 5-hydroxymethylcytosine residues in place of cytosine residues. Example from T4 phage: database code DCHM_BPT4, 246 amino acids (28.46 kDa); there is similarity to *Escherichia coli* **thymidylate synthase**.

DCMU *abbr. for* 3-(3,4-dichlorophenyl)-1,1-dimethylurea; a herbicide that blocks electron transport on the reducing side of photosystem II. One proprietary name is Diuron.



DCMU

Dco *symbol for* the decanoyl group, $CH_3-[CH_2]_8-CO-$.

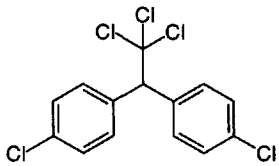
dCTP *abbr. for* deoxycytidine triphosphate, the common name for 2′-deoxycytidine 5′-triphosphate, 2′-deoxy-5′-cytidylyl diphosphate, cytosine 2′-deoxyriboside 5′-triphosphate.

dCyd *symbol for* a residue of the deoxynucleoside deoxycytidine; 2′-deoxyribosylcytosine; cytosine 2′-deoxyriboside (alternative to dC).

dCyd5′*P* *symbol for* deoxycytidine 5′-phosphate.

dd+ *abbr. for* dideoxy+ (def. 2); **1** used as a *prefix* to the appropriate three-letter or one-letter symbols for ribonucleosides in order to form symbols for 2′,3′-dideoxyribonucleosides (e.g. ddNuc *or* ddN, *symbol for* any (unknown or unspecified) 2′,3′-dideoxyribonucleoside; ddAdo *or* ddA, *symbol for* dideoxyadenosine). **2** used similarly to form abbreviations for 2′,3′-dideoxyribonucleoside 5′-triphosphates (e.g. ddNTP, *abbr. for* any (unknown or unspecified) 2′,3′-dideoxyribonucleoside 5′-triphosphate; ddCTP, *abbr. for* dideoxycytidine triphosphate).

DDT *abbr. and common name for* dichlorodiphenyltrichloroethane; 1,1,1-trichloro-2,2-bis(*p*-chlorophenyl)ethane; a contact insecticide that has proved particularly valuable in controlling insect disease vectors, especially mosquitoes (*Anopheles* spp.). However, it is toxic to higher animals as well. It has a very long persistence of activity from residual deposits which has caused it to be banned in many countries.



de+ *prefix (in organic chemical nomenclature)* denoting replacement of a specified group or atom in a specified chemical compound by a hydrogen atom. An exception is **deoxy+** when applied to hydroxy compounds, which denotes replacement of a hydroxyl group by a hydrogen atom. *See also* **dehydro+**, **des+**.

deacylase *informal name for* any enzyme that catalyses a deacylation reaction; it may be a hydrolase or a transferase.

deacylation the act or process of removing an acyl group from a chemical compound.

DEAD box a highly conserved motif in a family of putative RNA **helicases**, named after the single-letter code for the amino-acid sequence involved, i.e. Asp-Glu-Ala-Asp. The first DEAD-box protein that was shown to have RNA-helicase activity was the eukaryotic translational initiation factor eIF4-A. Other proteins have since been included in the family, based on sequence similarities; some have been shown to have ATP-dependent RNA-helicase activity, while in others this remains to be experimentally confirmed. *See also* **DEAH family**, **Appendix E**.

dead-end complex *an alternative name for* **abortive complex**.

DEAE *abbr. for* diethylaminoethyl, $(C_2H_5)_2N-CH_2-CH_2-$, a weakly basic group widely used as a substituent in hydroxylated chromatographic support matrices, e.g. cellulose, Sephadex, to form anion exchangers. *Compare* **QAE**.

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de-aerate to remove air from a liquid or a slurry, commonly by heating and/or reduction of pressure.

DEAH family yeast proteins that are structurally similar to **DEAD-box** proteins, but larger. They differ fom DEAD-box proteins in parts of the conserved region, especially in that they have a conserved DEAH sequence rather than DEAD. Some of them are known to be involved in RNA splicing, e.g. in *trans*-esterification steps and spliceosome release.

deamidase *name sometimes used for* an enzyme that catalyses the hydrolytic cleavage of the C–N bond in a carboxamide, but that is correctly termed an **amidase**.

deamidation the process of removing an amino group from an amide, either by hydrolysis or by a transfer reaction.

deaminase any of the enzymes that catalyse the nonoxidative removal of amino groups, with production of ammonia. They are usually aminohydrolase enzymes (sub-subclass EC 3.5.4), which hydrolytically deaminate amino-substituted cyclic amidines including various (free or combined) pterins, purines, or pyrimidines. Certain hydro-lyase (sub-subclass EC 4.2.1) and hydrolytic or nonhydrolytic ammonia-lyase (sub-subclass EC 4.3.1) enzymes also are commonly called deaminases.

deamination the process of removing an amino group from an organic compound. *Compare* **transamination**.

deaminooxytocin *or* **demoxytocin** a synthetic analogue of **oxytocin**, in which the N-terminal half-cystine residue has been replaced by a residue of 3-mercaptopropanoic acid. It is more potent than the parent compound.

de-ashing a procedure in which interfering inorganic (i.e., ash-forming) components are removed from samples of carbohydrates being analysed by liquid chromatography by passing them first through anion- and cation-exchange resins.

death domain a region of limited homology, consisting of about 80 residues close to the intracellular C terminus of certain cell-membrane receptors (e.g. the **TNF receptor**) that is essential for the receptors to generate a signal leading to apoptosis.

deblock to remove a **blocking group**. —**deblocking** *n*.

debrancher deficiency *an alternative name for* type III **glycogen** (storage) **disease**.

debranching enzyme any enzyme that catalyses the cleavage of branch points in particular branched biopolymers, e.g. **isoamylase**, **oligo-1,6-glucosidase** and **pullulanase**.

debye *symbol*: D; a non-SI unit of molecular dipole moment: $1\,D \approx 3.335\,64 \times 10^{-30}$ C m.

Debye, Petrus ('Peter') Josephus Wilhelmus (1884–1966), Dutch-born US physicist and physical chemist; Nobel Laureate in Chemistry (1936) 'for his contributions to our knowledge of molecular structure through his investigations on dipole moments and on the diffraction of X-rays and electrons in gases'.

Debye–Hückel theory a theory used to calculate the electric potential at a point in a solution in terms of the concentrations and charges of the ions and the properties of the solvent. It yields the logarithm of the mean rational activity coefficient:

$$\lg f^{+/-} = (A|z_1 z_2|\, I^{1/2})/(1 + BaI^{1/2}),$$

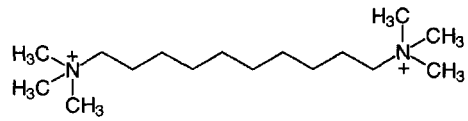
where the constants A and B involve the temperature and the dielectric constant of the solvent, a is an adjustable 'ion-size' parameter, I is the **ionic strength**, and $|z_1 z_2|$ is the absolute value of the valence product of the electrolyte under consideration. [After P. J. W. **Debye** and Eric Hückel (1896–1980), German physicist.]

dec+ *see* **deca+** (def. 2).

Dec *symbol for* the decyl group, CH_3–$[CH_2]_8$–CH_2–.

deca+ **1** *symbol*: da; the SI prefix denoting 10 times. **2** *or (before a vowel)* **dec+** *comb. form* denoting ten, tenfold, or ten times; formerly sometimes written as deka+ *or* dek+.

decamethonium *N,N,N,N*^{1},*N*^{1},*N*^{1}-hexamethyl-1,10-decanediaminium a nicotinic receptor ligand that causes sustained activation of the receptors, with consequent blockade of synaptic transmission (termed 'depolarizing block'). *See also* **suxamethonium**.



decanoate **1** the anion, CH_3–$[CH_2]_8$–COO^-, derived from decanoic acid (formerly capric acid). **2** any mixture of decanoic acid and the anion. **3** any salt or ester of decanoic acid.

decanoyl *symbol*: Dco; the univalent acyl group, CH_3–$[CH_2]_8$–CO–, derived from decanoic acid. *See also* **caproyl** (def. 1).

decant to pour off a supernatant liquid from a precipitate or other sediment. —**decantation** *n*.

decap to (enzymically) remove a **cap** (def. 1) from the 5′ end of a capped mRNA molecule. —**decapped** *adj*.

decapsidate to remove the capsid from a virus. —**decapsidation** *n*.

decarboxylase any of the enzymes of the sub-subclass EC 4.1.1, carboxy-lyases; they catalyse the removal of carboxyl groups from carboxylic acids.

decarboxylation the act or process of removing the carboxyl group from a carboxylic acid as carbon dioxide. The reaction may be enzyme-catalysed by a **decarboxylase** or, in some instances, particularly with 2-oxo acids, it may be spontaneous. —**decarboxylate** *vb.*; **decarboxylated** *adj*.

decay **1** a decrease in activity, force, quantity, or other physical attribute, especially with a characteristic time constant. **2** (**a**) **nuclear decay**: the spontaneous change of one nuclide into another, its daughter, with a different proton number or nucleon number. (**b**) **radioactive decay**: nuclear decay in which particulate or electromagnetic radiation (or both) is emitted, or in which spontaneous fission of the nucleus occurs. *See also* **disintegration**. **3** the decline of an atom or molecule from an excited state. **4** the biochemical decomposition of plant and animal remains, due chiefly to the activities of microorganisms.

decay accelerating factor *see* **complement decay-accelerating factor**.

decay constant *an alternative term for* **disintegration constant**.

deci+ **1** *symbol*: d; the SI prefix denoting 10^{-1} times. **2** *comb. form* denoting one tenth, one in ten.

decimolar *(informal)* one-tenth molar; i.e. denoting a solution of concentration 0.1 mol dm^{-3}.

decinormal *(informal; not now recommended)* one-tenth normal; i.e. denoting a solution of concentration 0.1 equivalents per litre (*see* **normal** (def. 2)).

Declomycin *proprietary name for* **demeclocycline**. *See also* **tetracycline**.

decoding *(informal) an alternative term for* **translation** (def. 1).

decontaminant an agent for removing or neutralizing a contaminant.

decontamination the act or process of removing or neutralizing any toxic or potentially toxic materials, or of reducing their concentrations to nonhazardous levels. The term is used especially in regard to microbes, toxic chemicals, carcinogens, and radioactive substances. *Compare* **contamination**.

decorin *or* **bone proteoglycan II precursor** a collagen-binding protein of the extracellular matrix, so called because it 'decorates' collagen fibrils. The core protein has a single **glycosaminoglycan** chain, together with other oligosaccharide substituents. Example from human: database code HSRNAFIB, 376 amino acids (43.10 kDa).

decose any **aldose** having a chain of ten carbon atoms in the molecule.

dCTP deaminase EC 3.5.4.13; *systematic name:* dCTP aminohydrolase; *other name*: deoxycytidine triphosphate deaminase.

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An enzyme that hydrolyses the amino group of dCTP to form dUTP and NH_4^+. Example from *Escherichia coli*: database code DCD_ECOLI, 193 amino acids (21.23 kDa).

deculose any **ketose** having a chain of ten carbon atoms in the molecule.

decyl *symbol*: Dec; the alkyl group, CH_3–$[CH_2]_8$–CH_2–, derived from decane.

***n*-decyl-β-D-glucopyranoside** a nonionic detergent, useful for solubilizing membrane proteins; CMC 2–3 mM.

***n*-decyl-β-D-maltopyranoside** a nonionic detergent, useful for solubilizing membrane proteins; CMC 1.6 mM.

dedifferentiation the loss of the characteristics of a specialized cell and regression to a simpler state. —**dedifferentiate** *vb.*

de Duve, Christian René Marie Joseph (1917–), Belgian biochemist and cell biologist distinguished for his discoveries of the lysosome and the peroxisome and for studies of their properties in health and disease; Nobel Laureate in Physiology or Medicine (1974) jointly with A. Claude and G. E. Palade 'for their discoveries concerning the structural and functional organization of the cell'.

defective virus a virus that is unable to reproduce itself whilst infecting a cell without the presence of a **helper virus**.

defensin any of a family of small cationic peptides, containing six cysteines in disulfide linkage, that have broad-spectrum antibiotic action and contribute to host defence against microorganisms. They are abundant in phagocytes and small intestinal mucosa of humans and other mammals and in the hemolymph of insects. Defensins adopt multimeric pore-forming complexes in membranes, thereby rendering the membrane permeable. They are distinguished by a predominantly **beta-sheet** structure. Examples, β-defensin 1 from *Bos taurus*: database code BD01_BOVIN, 38 amino acids (4.28 kDa); hemolymph defensin from *Mytilus galloprovincialis*: database code DEFI_MYTGA, 38 amino acids (4.27 kDa).

deficiency disease any disease resulting from the deficiency of one or more essential nutrients, e.g. a vitamin, an essential amino acid, or an essential mineral.

deficient lacking some essential component; inadequate in amount. The term can be used, e.g., for a deficient (culture) medium, deficient diet, or deficient strain (of an organism).

defined medium any culture medium in which the concentrations of all the constituents, including trace substances, are quantitatively known.

deformylase *see* **formylmethionine deformylase**.

degeneracy **1** *(in a code)* the existence of two or more synonyms specifying a particular item or function; *see also* **degenerate code**. **2** *(in a quantized system)* the existence of two or more linearly independent **eigenfunctions** with the same **eigenvalue**, especially the condition of an atom or molecule. **3** *(of an atom or molecule)* the condition in which the energy levels of different quantum states have the same energy level. —**degenerate** *adj.*

degenerate code a code in which more than one symbol represents the same entity. One such is the **genetic code**, wherein a specific amino acid may be encoded by two or more nucleotide triplets, or **codons** present in a nucleic acid or polynucleotide.

degeneration the process whereby a cell, tissue, or organ changes to a less specialized or functionally less active form.

degradation *(in chemistry)* **1** the gradual stepwise and deliberate conversion of a molecule into smaller chemical entities, commonly to elucidate its chemical structure. **2** any undesired breakdown of a molecule or material with impairment or loss of its characteristic properties. **3** depolymerization; decomposition. **4** *(in biochemistry)* catabolism.

degranulation **1** any process by which granular cells lose their granules. **2** the stripping of polysomes from rough endoplasmic reticulum *in vitro*.

degree *see* **angle**, **temperature**.

degree Celsius *symbol*: °C; the SI derived unit of **Celsius temperature**. It denotes the same interval of temperature as the **kelvin** on a scale with different reference points.

degree of polymerization the number of **monomeric units** in the molecule of a polymer.

degrees of freedom **1** *(in statistics)* the number of unrestricted independent variables constituting a statistic; thus in a sample of n values of x there are n deviations $(x_i - \bar{x})$, where $\bar{x}$ is the estimate of the mean, used in calculating the sample **variance**, s^2, but they are not all independent, since there is a linear relation connecting them, namely:

$$\sum_{i=1}^{n} (x - \bar{x}) = 0$$

hence only $(n - 1)$ of the quantities are independent, and there are $(n - 1)$ degrees of freedom in the calculation of s^2. **2** *(in physics)* the minimum number of parameters necessary to the description of the state of a system. **3** the number of independent equations by which the energy of a system may be expressed. **4** *(in chemistry)* the number of independently variable intensive properties that must be specified in order to describe completely the state of the system. *See* **phase rule**.

de Hevesy *see* **Hevesy**.

dehydrase *obsolete term for* **dehydratase** or **dehydrogenase**.

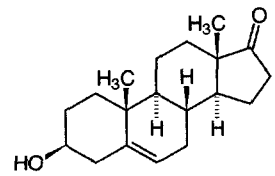
dehydratase *or (formerly)* **dehydrase** any hydro-lyase enzyme, of sub-subclass EC 4.2.1, that catalyses the (reversible) breakage of a carbon–oxygen bond leading to the formation of an unsaturated product and the elimination of water; e.g. citrate dehydratase, EC 4.2.1.4. When named after the alternative, i.e. unsaturated, substrate, the enzyme is termed a **hydratase**; e.g. aconitate hydratase, EC 4.2.1.3. *See also* **carbonate dehydratase**.

dehydration **1** the removal of combined, or adsorbed, water from a chemical compound; *see also* **anhydrous**. **2** the process or result of losing water, especially the abnormal loss of water from an organism. **3** the replacement of water by solvents.

dehydro+ *prefix (in chemical nomenclature)* denoting the loss of two hydrogen atoms. In common usage it is often used in place of **didehydro+**; e.g. 7,8-didehydrocholesterol is often termed dehydrocholesterol. *Distinguish from* **anhydro+**.

2-dehydro-3-deoxyphosphooctonate aldolase *another name for* **3-deoxy-D-*manno*-octulosonic acid 8-phosphate synthase**.

dehydroepiandrosterone *abbr.*: DHEA; androstenolone, *trans*-dehydroandrosterone (*abbr.*: DHAS), 3β-hydroxyandrost-5-en-17-one; an intermediate in androgen and estrogen biosynthesis, formed from 17α-hydroxypregnenolone in testis, ovary, and adrenal cortex by the action of 17α-hydroxyprogesterone aldolase, EC 4.1.2.30. It is the immediate precursor of androstenedione, which is formed from it by the action of 3β-hydroxy-Δ^5-steroid dehydrogenase, EC 1.1.1.145 and it can be converted to androst-5-en-17-one 3β-sulfate (DHEA-S), in which form it is measured in plasma, there being about 1000 times more DHEA-S than DHEA in plasma.



dehydrogenase any donor:acceptor **oxidoreductase** enzyme, of the class EC 1, when named after the alternative, i.e. more reduced, substrate and when dioxygen is not the acceptor.

dehydrogenate to oxidize an organic compound by the removal of one or more hydrogen atoms. —**dehydrogenation** *n.*

3-dehydroquinate dehydratase EC 4.2.1.10; *systematic name*: 3-dehydroquinate hydro-lyase; *other name*: 3-dehydroquinase; an enzyme that catalyses the reaction:

3-dehydroquinate = 3-dehydroshikimate + H_2O.

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The reaction forms part of the **shikimate pathway**. For example, *see* ***aro1***. *See also* **pentafunctional arom polypeptide**.

3-dehydroquinate synthase EC 4.6.1.3; an enzyme that catalyses the hydrolysis of 7-phospho-3-deoxy-*arabino*-heptulosonate to 3-dehydroquinate and orthophosphate. *See* **pentafunctional arom polypeptide**; **shikimate pathway**.

(3-)dehydroretinal *an alternative name for* **3,4-didehydroretinal** (not recommended, except for nutritional usage).

(3-)dehydroretinoic acid *an alternative name for* **3,4-didehydroretinoic acid** (not recommended, except for nutritional usage).

(3-)dehydroretinol *an alternative name for* **3,4-didehydroretinol** (not recommended except for nutritional usage).

deionize *or* **deionise** to remove all ions from a solution. —**deionization** *or* **deionisation** *n*. *See also* **desalt**.

deionizer *or* **deioniser** a device used to remove ions from solutions, usually by the use of **ion exchangers**.

Deisenhofer, Johann (1943–), German-born US biochemist; Nobel Laureate in Chemistry (1988) jointly with R. Huber and H. Michel 'for the determination of the three-dimensional structure of a photosynthetic reaction centre'.

deka+ *or (before a vowel)* **dek+** *former spelling of* **deca+** (def. 2).

delayed early gene *see* **early gene**.

delayed hypersensitivity *or* **type IV hypersensitivity** *(in immunology)* a **hypersensitivity** reaction that arises more than a day after encounter with the antigen and is mediated by antigen-sensitized $CD4^+$ T cells that release **cytokines**, attracting macrophages to the site and activating them. This type of hypersensitivity is seen in skin contact reactions and in response to some chronic pathogens such as those that cause leprosy, tuberculosis, and schistosomiasis. *Compare* **immediate hypersensitivity**.

Delbrück, Max (1906–81), German-born US physicist, molecular geneticist, and sensory physiologist; notable in particular for his development of the plaque technique for studying viruses and for his research on the interaction of bacteriophages with bacteria; Nobel Laureate in Physiology or Medicine (1969) jointly with A. D. Hershey and S. E. Luria 'for their discoveries concerning the replication mechanism and the genetic structure of viruses'.

deletion the loss of a segment of genetic material from a chromosome. A deletion can vary in size from a single nucleotide residue to a segment containing a number of genes. A **terminal deletion** occurs at one end of the chromosome, whereas an **intercalary deletion** occurs elsewhere along the chromosome.

delipidation the removal of lipid from a sample.

deliquescent *(of certain salts)* tending to absorb water from the surrounding atmosphere at ordinary temperature and pressure and then to dissolve in the water so taken up. *Compare* **hygroscopic**. —**deliquesce** *vb.*; **deliquescence** *n.*

delocalization *or* **delocalisation** a quantum-mechanical concept implying that the unpaired electron density in a molecule is spread over several atoms. Analogously, delocalization of the spin of an unpaired electron can occur.

delta *symbol*: δ (lower case) *or* Δ (upper case); the fourth letter of the Greek alphabet. For uses *see* **Appendix A**.

deltahedron (*pl.* **deltahedra**) any polyhedron whose faces are all equilateral triangles. Some viruses disaggregate to form particles that are deltahedra. —**deltahedral** *adj.*

deltakephalin (D-Thr^2)-Leu-enkephalin-Thr; a highly potent and specific synthetic hexapeptide δ-opiate receptor agonist; structure Tyr-D-Thr-Gly-Phe-Leu-Thr. *See also* **enkephalin**.

delta-sleep-inducing peptide *or* **sleep peptide** a nonapeptide, Trp-Ala-Gly-Gly-Asp-Ala-Ser-Gly-Glu, found in the plasma of rats and rabbits, that shows a several-fold increase in concentration during sleep. It rapidly induces slow-wave (i.e. delta) sleep on injection into awake animals.

dematin a protein involved in the formation of actin bundles, abundantly expressed in brain, heart, skeletal muscle, kidney, and lung, whose activity is abolished upon phosphorylation by cAMP-dependent protein kinase. It is a member of the **villin** family. Example from human: database code DEMA_HUMAN, 383 amino acids (43.07 kDa).

demeclocycline 6-demethyl-7-chlorotetracycline; *see* **tetracycline**.

demethylation any reaction involving the removal of one or more methyl groups from a molecule, whether by oxidation or transfer to an acceptor molecule.

demineralization *or* **demineralisation** **1** the process of removing inorganic salts, e.g. from water or other liquid; deionization. **2** excessive loss of mineral salts from the tissues, especially bone, as occurs in certain diseases.

demoxytocin *an alternative name for* **deaminooxytocin**.

denaturation **1** *(of a protein)* a process in which the three-dimensional shape of a molecule is changed from its **native state** without rupture of peptide bonds. It is sometimes taken to include disulfide bond rupture or chemical modification of certain groups in the protein if these processes are also accompanied by changes in its overall three-dimensional structure. Denaturation is frequently irreversible and accompanied by loss of solubility (especially at the isoelectric point) and/or of biological activity. **2** *(of a nucleic acid)* a process whereby a molecule is converted from a firm, two-stranded, helical structure to a flexible, single-stranded structure. *Compare* **renaturation**.

denaturation loop a non-base-paired interstrand loop formed in the more thermally unstable regions (i.e., of high A+T content) of a duplex DNA molecule during **melting** (def. 3).

denaturation mapping the identification of regions of low thermal (or alkali) stability (i.e., of high A+T content) in a duplex DNA molecule, by trapping the partly melted structure and blocking renaturation, e.g. with formaldehyde (which preferentially couples with the amino groups of the single-stranded regions), and subsequently examining the specimen by electron microscopy.

dendrite a freely branching protoplasmic process of a nerve cell that transmits nerve impulses to the body of the cell and that communicates functionally with dendrites or bodies of other nerve cells.

dendrogram any branching treelike diagram that illustrates the relationships between organisms or objects.

Denhardt's solution a buffer, containing Ficoll, polyvinylpyrrolidine, and bovine serum albumin, that is used as a blocking reagent for **hybridization** with nitrocellulose filters. [After David Tilton Denhardt (1939–), US biochemist.]

denitrification the reduction, especially by denitrifying bacteria, of simple inorganic nitrogen compounds, such as nitrates and nitrites, to gaseous products such as nitric oxide, nitrous oxide, and/or dinitrogen. *See also* **nitrate reduction**. *Compare* **nitrification**, **nitrogen fixation** (def. 1).

denitrifying bacteria soil bacteria that, in the absence of dioxygen, reduce nitrates and nitrites to gaseous products. *Compare* **nitrifying bacteria**.

de novo *Latin* anew, from the beginning; e.g. *de novo* synthesis.

densimeter *an alternative name for* **densitometer** (def. 2).

densitometer **1** *or* **photodensitometer** an apparatus for measuring the extent to which a material absorbs light (*see* **absorptiometer** (def. 1)) or reflects light (*see* **reflectometer**). It is useful for scanning chromatograms or electrophoretograms, for determining the opacity of solutions or suspensions, or for measuring the blackening of photographic films. **2** *or* **densimeter** an instrument for measuring the mass density or relative density of liquids or gases. —**densitometry** *n.*; **densitometric** *adj.*

density **1** **a** *or* **mass density** *symbol*: ρ; the mass of a substance per unit volume. **b** *or* **linear density** *symbol*: ρ_l; the mass of a substance per unit length. **c** *or* **surface density** *symbol*: ρ_A *or* ρ_S; the mass of a substance per unit area. *Compare* **relative density**. **2** the distribution of a scalar physical quantity per unit area of space (e.g. radiant energy density) or per unit volume (e.g. charge density). **3** the distribution of a vector physical quan-

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tity per unit area of space (e.g. electric current density, magnetic flux density). **4 optical density**. *See* **absorbance**.

density-gradient centrifugation *see* **isopycnic centrifugation**.

density-gradient sedimentation equilibrium *see* **isopycnic centrifugation**.

density-marker bead any small coloured bead of accurately known mass density that is used for calibrating density gradients. Generally a set of several such beads, covering a range of densities, is used.

dentate having teeth or toothlike projections. *See also* **multidentate**.

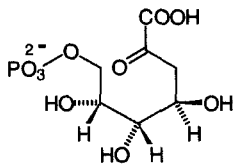
denticity the number of distinct but linked atoms of a specified ligand binding to the central atom in a coordination entity. *Compare* **ligancy**.

dentine *or* **dentin** the hard, dense, calcified tissue of a tooth lying between the enamel and the pulp. It is 75% mineral, mainly hydroxyapatite.

deoxy+ *or (formerly)* **desoxy+** *prefix (in organic chemical nomenclature)* **1** denoting the replacement of a hydroxyl group by a hydrogen atom; *see also* **de+**. **2** (*abbr.*: d+) indicating the presence of one or more residues of 2-deoxy-D-ribose. *Compare* **ribo+** (def. 2). **3** used especially with hemoglobin, to signify absence or removal of dioxygen. *Compare* **oxy+**.

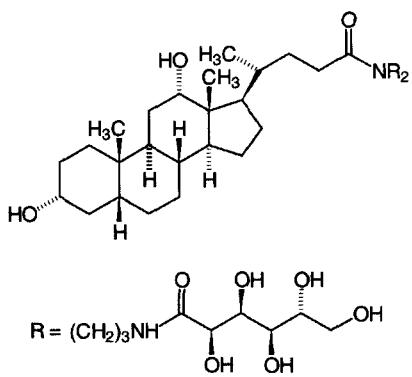
5′-deoxy-5′-adenosylcobalamin *or* **adenosylcobalamin** *see* **cobamide coenzyme**.

3-deoxy-D-*arabino*-(2-)heptulosonate 7-phosphate *or (less formally)* **3-deoxy-D-*arabino*-heptulosonate 7-phosphate**; *abbr.*: DAHP; an early intermediate in aromatic amino acid biosynthesis by the **shikimate pathway** in autotrophic organisms.

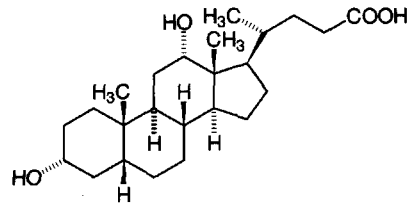


α-pyranose form

deoxy-BigCHAP *N,N-bis*-(3-D-gluconamidopropyl)-(7-deoxy)-cholamide; a nonionic detergent analogue of **CHAPS**, **CHAPSO**, and **BigCHAP**; aggregation number 8–16; CMC 1.1–1.4 mM.

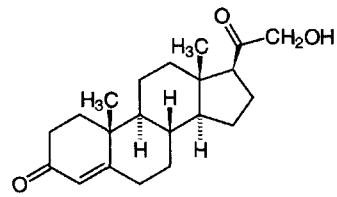


deoxycholic acid 3α,12α-dihydroxy-5β-cholan-24-oic acid; one of the **bile acids** occurring as its conjugate with glycine or taurine in the bile of most mammals, including dog, goat, human, ox, sheep, and rabbit. The sodium salt, sodium deoxycholate, is used as a detergent. Aggregation number 3–12; CMC 2–6 mM.



deoxycholic acid

deoxycorticosterone *abbr.*: DOC; Kendall's desoxy compound B, Reichstein's substance Q, 21-hydroxyprogesterone, 21-hydroxypregn-4-ene-3,20-dione; a ***mineralocorticoid*** hormone with little glucocorticoid activity, synthesized by the adrenal gland. For clinical purposes it may be administered as its ester, deoxycorticosterone acetate (*abbr.*: doca *or* DOCA).



deoxycytidine deaminase *see* **cytidine deaminase**.

deoxycytidylate deaminase *an alternative name for* dCMP deaminase.

3-deoxy-D-*manno*-octulosonic acid 8-phosphate synthase EC 4.1.2.16; *recommended name*: 2-dehydro-3-deoxyphosphooctonate aldolase; *other name*: phospho-2-keto-3-deoxyoctonate (*abbr.*: phosphoKDO) aldolase; an enzyme that catalyses the formation of 3-deoxy-D-*manno*-octulosonic acid 8-phosphate from D-arabinose 5-phosphate and phospho*enol*pyruvate with release of orthophosphate. It is the first step in the biosynthesis of the bacterial lipopolysaccharide, lipid A, and is required for cell growth. Example from *Escherichia coli*: database code KDSA_ECOLI, 284 amino acids (30.80 kDa).

deoxynojirimycin an antibiotic produced by *Bacillus* species, the reduced form of **nojirimycin**; it inhibits formation of N-linked complex oligosaccharides in culture.

deoxynucleoside *an alternative name for* **deoxyribonucleoside**.

deoxynucleotide *an alternative name for* **deoxyribonucleotide**.

deoxynucleotidyltransferase EC 2.7.7.31; *recommended name*: DNA nucleotidylexotransferase; *other names*: terminal addition enzyme; terminal transferase; terminal deoxyribonucleotidyltransferase. It is a Mg^{2+}-dependent polymerase enzyme that extends the 3′ end of a DNA strand one nucleotide at a time, independent of a template. It catalyses the reaction (if *n* nucleotides are added in all):

$$n\ (\text{deoxynucleoside triphosphate}) + (\text{deoxynucleotide})_m = n\ (\text{pyrophosphate}) + (\text{deoxynucleotide})_{m+n}.$$

Example (bovine): database code TDT_BOVIN, 520 amino acids (59.60 kDa).

deoxypentose any monosaccharide in which one alcoholic hydroxyl group of a pentose has been replaced by a hydrogen atom.

deoxypentose nucleic acid *former term for* **deoxyribonucleic acid**.

deoxypolymeric tailing extension of the 3′ end of a strand of DNA, or of each strand of (a fragment of) duplex DNA, by a tail comprising a homooligomer or homopolymer of a deoxyribonucleotide. It is effected by the enzyme **deoxynucleotidyl**

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transferase. The process is useful for forming cohesive termini to DNA fragments in the preparation of **recombinant DNA**. *See* **cohesive end**.

deoxyribonuclease *abbr.*: DNase (*or sometimes* DNAse *or* DNAase); any enzyme within subclass EC 3.1, esterases, that catalyses the hydrolytic cleavage of phosphodiester linkages in DNA. If such an enzyme catalyses endonucleolysis (i.e. hydrolysis of nonterminal phosphodiester linkages) it is termed an **endodeoxyribonuclease**; if it catalyses exonucleolysis (i.e. hydrolysis of terminal linkages) it is termed an **exodeoxyribonuclease**. *See also* **AP endonuclease, crossover point, deoxyribonuclease I, deoxyribonuclease II, deoxyribonuclease III, deoxyribonuclease IV (phage T4-induced), deoxyribonuclease V, deoxyribonuclease X, deoxyribonuclease KI, deoxyribonuclease (pyrimidine dimer), endonuclease, exodeoxyribonuclease I, exodeoxyribonuclease V, exodeoxyribonuclease VII, exodeoxyribonuclease (phage SP3-induced), *myt5*, restriction enzyme**.

deoxyribonuclease I EC 3.1.21.1; *other names*: pancreatic DNase; DNase; thymonuclease. An enzyme that catalyses the endonucleolytic cleavage of DNA to 5′-phosphodinucleotide and 5′-phosphooligonucleotide end products. It shows a preference for double-stranded DNA. Example from *Bos taurus*: database code DRN1_BOVIN, 260 amino acids (29.06 kDa). *See also* **streptodornase**.

deoxyribonuclease II EC 3.1.22.1; *other names*: DNase II; pancreatic DNase II. An enzyme that catalyses endonucleolytic cleavage of DNA to 3′-phosphomononucleotide and 3′-phosphooligonucleotide end products.

deoxyribonuclease III EC 3.1.11.2; *other name*: exonuclease III. An enzyme that catalyses exonucleolytic degradation of double-stranded DNA progressively in the 3′- to 5′-direction, releasing 5′-phosphomononucleotides. Example endodeoxyribonuclease III from *Escherichia coli*: database code EX3_ECOLI, 268 amino acids (30.91 kDa); this enzyme is also the major **AP endonuclease** (i.e. an endonuclease) in *E. coli*.

deoxyribonuclease IV (phage T4-induced) EC 3.1.21.2; *other names*: endodeoxyribonuclease IV (phage T4-induced); endonuclease IV. An enzyme that catalyses endonucleolytic cleavage of DNA to 5′-phosphooligonucleotide end products. Example from *Bacillus subtilis*: database code END4_BACSU, 297 amino acids (33.07 kDa).

deoxyribonuclease V EC 3.1.22.3; *other name*: endodeoxyribonuclease V. An enzyme that catalyses endonucleolytic cleavage at apurinic or apyrimidinic sites within DNA to yield products with a 3′-phosphate. It is involved in DNA repair. The enzyme from *Escherichia coli* consists of three subunits, RECB, RECC, and RECD, also known as the β chain, γ chain, and α chain, respectively. Example, α chain: database code EX5A_ECOLI, 608 amino acids (66.96 kDa).

deoxyribonuclease X EC 3.1.22.5; an enzyme that catalyses endonucleolytic cleavage of supercoiled plasmid DNA to produce linear DNA duplexes.

deoxyribonuclease K1 *or* ***Aspergillus*** **deoxyribonuclease K1** EC 3.1.22.2; *other name*: *Aspergillus* DNase K1. An enzyme that catalyses endonucleolytic cleavage of DNA to 3′-phosphomononucleotide and 3′-phosphooligonucleotide end products.

deoxyribonuclease (pyrimidine dimer) EC 3.1.25.1; *other name*: endodeoxyribonuclease (pyrimidine dimer). An enzyme involved in DNA repair; it can induce single-strand breaks in DNA on the 5′-side of pyrimidine dimers in the strand containing the lesion, after formation of the dimers as a result of, e.g., ultraviolet radiation.

deoxyribonucleate **1** *abbr.*: DNA; any anionic form of deoxyribonucleic acid. **2** any salt of deoxyribonucleic acid.

deoxyribonucleic acid *former names*: desoxyribonucleic acid *or* thymonucleic acid; *also* deoxypentose nucleic acid *or* deoxyribose nucleic acid *or* desoxyribose nucleic acid *or* thymus nucleic acid. *See* **DNA**.

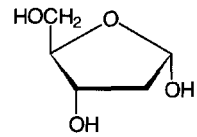
deoxyribonucleoprotein *abbr.*: DNP; any conjugated protein that contains DNA as the nonprotein moiety.

deoxyribonucleoside *or* **deoxynucleoside** any **nucleoside** (def. 1) in which the glycose moiety is 2-deoxy-β-D-ribofuranose.

deoxyribonucleoside monophosphate kinase any of several enzymes within sub-subclass EC 2.7.4 that catalyse the transfer of a phosphoric residue from a nucleoside triphosphate to a deoxyribonucleoside monophosphate, e.g. from ATP to a deoxyribonucleoside phosphate to form ADP and a deoxyribonucleoside diphosphate.

deoxyribonucleotide *or* **deoxynucleotide** a deoxyribonucleoside in ester linkage to phosphate, commonly at the 5′ position of its deoxyribose moiety. *See* **nucleotide**.

deoxyribose **1** *symbol*: dRib; *the trivial name for* 2-deoxyribose; 2-deoxy-*erythro*-pentose. The D enantiomer, as 2-deoxy-β-D-ribofuranose, forms the glycose moiety of all deoxyribonucleosides, deoxyribonucleotides, and deoxyribonucleic acids. **2** 3-deoxyribose (*see* **cordycepose**).



2-deoxy-α-D-ribofuranose

deoxyribose nucleic acid *former name for* **deoxyribonucleic acid**.

deoxyriboside any glycoside or glycosylamine in which deoxyribose forms the glycose moiety, especially a deoxyribonucleoside.

deoxyribosome *see* **nu body**.

deoxyribosylthymine *an alternative name for* thymidine.

deoxyribotide any deoxyriboside esterified with phosphate at the 5′ position on its ribose moiety, especially a deoxynucleotide.

deoxyribovirus *an alternative name for* **DNA virus**.

deoxysaccharide *or* **deoxysugar** any saccharide in which one alcoholic hydroxyl group has been replaced by a hydrogen atom.

depactin a protein isolated from starfish eggs, able to depolymerize F-actin and inhibit the extent of actin polymerization. It binds to actin monomers from filaments and in solution. Example from *Asterias amurensis*: database code DEPA_ASTAM, 150 amino acids (17.21 kDa).

dependent form of glycogen synthetase the phosphorylated form of the enzyme glycogen synthetase that is 'dependent' for its activity on the presence of glucose 6-phosphate, a positive effector.

dependent variable any variable in a mathematical statement or equation whose value depends on the values taken by the related independent variables.

dephospho-[reductase kinase] kinase EC 2.7.1.110; *other name*: reductase kinase kinase; an enzyme that catalyses the phosphorylation of dephospho-[[3-hydroxy-3-methylglutaryl-CoA reductase (NADPH)] kinase] by ATP with release of ADP. It is involved in the regulation of **hydroxymethylglutaryl-CoA reductase** (HMGCoA reductase). By phosphorylating reductase kinase, it activates that enzyme to phosphorylate HMGCoA reductase, thereby inactivating the latter.

dephosphorylation the process of removing one or more phosphoric (ester or anhydride) residues from a molecule.

depolarization *or* **depolarisation** **1** a reduction in the electric potential measured across a cell membrane, especially that brought about in a nerve or muscle cell by an electrical stimulus or a drug. **2** the decrease of the angle of polarization of polarized light so that it appears altered when viewed through an analyser. *See also* **fluorescence depolarization**.

depolarization ratio *or* **depolarisation ratio** *(in light scattering)* the ratio of the horizontally to the vertically polarized

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components of the light scattered by scattering particles when illuminated by unpolarized light. If the scattering particles are isotropic the depolarization ratio will be zero; if they are anisotropic it will not be zero.

deproteinization *or* **deproteinisation** the process of removing protein from a biological sample, either by precipitation of protein from solution or by hydrolysis of protein with proteolytic enzymes.

depside any of a family of natural or artificial compounds derived from two or more molecules of various trihydroxybenzoic acids by esterification of a carboxyl group on one molecule with a hydroxyl group on another molecule (which may or may not be of the same structure as the first). By analogy with peptides, depsides derived from two, three, etc., or several trihydroxybenzoic acid units may be termed **didepside**, **tridepside**, etc., or **polydepside**, respectively. Depsides occur widely in lichens and also as components of some tannins.

depsidone any compound derived from two phenolcarboxylic acid molecules (which may or may not be the same molecules) that are joined together by both an ester and an ether link. Such substances are found in lichens.

depsipeptide any linear or macrocyclic compound containing (alternating) amino-acid and hydroxy-acid residues, linked by amide, *N*-methylamide, and ester bonds. Among the naturally occurring **cyclodepsipeptides** (sometimes alternatively termed peptolides) are the antibiotics **valinomycin**, the **enniatins**, and the monamycins.

depurinate to remove purine residues from a polynucleotide. —**depurinated** *adj.*; **depurination** *n.*

depyrimidinate to remove pyrimidine residues from a polynucleotide. —**depyrimidinated** *adj.*; **depyrimidination** *n.*

derepression the phenomenon in which a repressor is prevented from interacting with the operator component of an **operon** and an increase in the synthesis of a gene product thereby occurs. With an inducible enzyme, the inducer derepresses the operon. Derepression may also result from mutations, either in the **regulator(y) gene**, thus blocking repressor synthesis, or in the operator gene, thus rendering it insensitive to the repressor.

deRib *(sometimes) symbol for* 2-deoxy-D-ribose (dRib is the correct symbol).

derivative **1** any compound that may, at least theoretically, be formed from another compound to which it is structurally related. **2** *see* **derivative of a function**.

derivative of a function *(in mathematics)* the limit of the ratio of an increment of a dependent variable to the corresponding increment of an associated independent variable as the latter increment tends to zero.

derivatize *or* **derivatise** to convert a chemical compound into a derivative. —**derivatization** *or* **derivatisation** *n.*

dermaseptin any of a series of antimicrobial peptides derived from amphibian skin. Dermaseptins s1–5 constitute a family of cationic lysine-rich amphipathic antifungal peptides of 28–34 residues. Presumed to protect the naked frog skin from infections, they have wider application, being the first vertebrate peptides to show lethal effects against the filamentous fungi that can cause infections in immunodeficiency syndrome, or during the use of immunosuppressive agents. *Compare* **magainin**.

dermatan sulfate *or* **chondroitin sulfate B** any of a group of glycosaminoglycans with repeats consisting of β1→4-linked L-iduronyl-(β1→3)-*N*-acetyl-D-galactosamine 4-sulfate units. They are important components of ground substance or intercellular cement of skin and some connective tissues (*see* **matrix** (def. 3)). They usually occur attached to proteins as proteoglycans, the mode of linkage being the same as for **chondroitin sulfate**. A hereditary deficiency in the ability to degrade dermatan sulfate characterizes certain types of **mucopolysaccharidosis**.

dermis *or* **corium** the thick layer of tissue forming part of the skin and lying beneath the epidermis. It consists of loose connective tissue in which are blood capillaries, smooth-muscle fibres, sweat glands and sebaceous glands with their ducts, hair follicles, and sensory nerve endings. —**dermal**, **dermic** *adj.*

dermorphin any of a group of heptapeptide amides of the general structure H-Tyr-DAla-Phe-Gly-Tyr-Xaa-Ser-NH_2, isolated from the skin of frogs of the genus *Phyllomedusa* and some other amphibians; they show high and long-lasting opiate-like activity.

DES *abbr. for* diethylstilbestrol.

des+ *prefix* **1** (in the trivial name of a polycyclic compound, e.g. a steroid) indicating the removal of a terminal ring, with addition of a hydrogen atom at each junction arm with the adjacent ring; it should be followed by the italic capital letter designating the terminal ring in question, e.g. des-*A*-androstane. **2** (in the trivial name of a polypeptide) indicating the removal of an amino-acid residue, terminal or otherwise; it should be followed by the name or symbol for the amino acid in question and an arabic number indicating its position in the normal polypeptide, e.g. des-7-proline-oxytocin, or des-Pro^7-oxytocin. **3** indicating the removal of a specified atom or group from a molecule of an indicated substance; *see* **desamido+**, **desthio+**; *see also* **descarboxy-clotting factor**. **4** *(formerly) a variant of* **de+** (still preferred in some languages, e.g. French, German).

desalinate to remove salt, especially from seawater to render it suitable for drinking or irrigation. *Compare* **desalt**. —**desalination** *n.*

desalt to remove small, usually inorganic ions from a sample. Methods that may be used include electrodialysis, electrophoresis, gel filtration, and ion-exchange chromatography. *See also* **deionize**. *Compare* **desalinate**.

desamidation the hydrolysis of one or more carboxamide groups in a molecule to carboxyl groups.

desamido+ *prefix* indicating **desamidation** of a molecule, especially of a peptide.

desaturase *general name for* any enzyme catalysing a desaturation reaction. The name specifically often refers to any of several fatty-acyl-CoA desaturases, enzymes coming within subsubclass EC 1.14.99; in animals these are associated with the endoplasmic reticulum, require dioxygen, and insert double bonds into saturated and *Z*(i.e. *cis*)-unsaturated fatty acids. They also occur in higher plants, protozoa, and fungi. These enzymes are specific for position in the fatty-acyl chain, and are termed Δ^5-desaturase, Δ^9-desaturase, and so on, according to the distance from the carboxyl carbon atom to the first carbon atom of the double bond. In mammals, there is a lack of any desaturase that inserts a double bond nearer to the terminal methyl group of the fatty acid than nine carbon atoms, hence the need for *n*-3 and *n*-6 precursor fatty acids (the **essential fatty acids**). *See also* **linoleic family**, **linolenic family**.

desaturation **1** any process or reaction in which an organic compound becomes **unsaturated** (def. 2), e.g. by removal of two hydrogen atoms, or a hydrogen atom and a hydroxyl group, from adjacent carbon atoms. **2** any process in which ligands are removed from a macromolecule so that all the binding sites for that ligand are no longer occupied. —**desaturate** *vb.*; **desaturated** *adj.*

descarboxy-clotting factor any of the abnormal blood clotting factors containing glutamic acid residues instead of γ-carboxyglutamic-acid residues. They are formed in animals deficient in vitamin K or during administration of vitamin K antagonists. *Compare* **PIVKA**.

Descartes, René (1596–1650), French philosopher and mathematician. *See also* **Cartesian**.

descending chromatography any chromatographic technique in which a liquid mobile phase runs downwards through the supporting matrix.

descriptive name name of an organic substance that is more descriptive of action or function and often more convenient than its **trivial name**, **semisystematic name**, **systematic name**, or other type of name permitted by the rules of chemical nomenclature.

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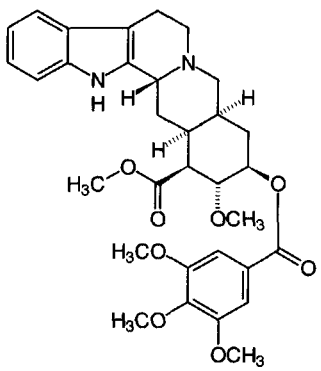
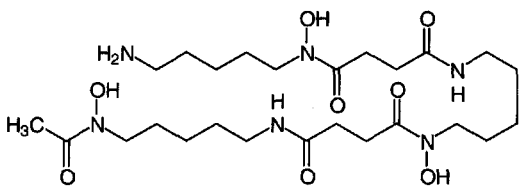
desensitization *or* **desensitisation** **1** a spontaneous decline in response resulting from continuous application of agonist, or to repeated applications or doses; such attenuation may result within minutes of prior stimulation, or may take hours to develop. It is recommended that this term be used where **fade** or **tachyphylaxis** are considered to involve the receptor itself, or to be a direct consequence of receptor activation. **Homologous desensitization** results from prior stimulation with the receptor's own agonist, whereas **heterologous desensitization** results from the activity of other agonists acting at other receptors. On the longer time scales, desensitization may result from receptor internalization in **coated pits**, and over shorter time scales from modification of the receptor in a way that uncouples it from signal transduction systems, e.g. by phosphorylation (*see* **adrenergic receptor kinase**). **2** the modification of an enzyme, either by mutation or chemically, so that it no longer responds to **effectors** but retains its catalytic activity. **3** the suppression of an established (immunological) hypersensitivity by injection of antigen, usually in very small doses. In delayed hypersensitivity the antigen reacts with sensitized cells, so neutralizing them. In immediate hypersensitivity the antigen either causes blocking antibody production (in atopy) or forms nontoxic complexes with existing antibodies (in anaphylaxis). —**desensitize** *vb.*; **desensitized** *adj.*

deserpidine desmethoxyreserpine, 11-desmethoxy-*O*-(3,4,5-trimethoxybenzoyl)reserpic acid methyl ester; an alkaloid derived from roots of *Rauwolfia canescens* with pharmacological actions similar to the parent methoxy compound, **reserpine**.



desferrioxamine a siderophore of the hydroxamate type derived from *Streptomyces pilosus* that forms a chelate complex specifically with Fe(III) ions, yielding **ferrioxamine**. It is used parenterally to treat acute iron poisoning and to reverse iron and aluminium overload. Its natural function is to transport iron into the microbial cell and/or to make iron available for the synthesis of heme.



desiccant a substance such as $CaCl_2$ or P_2O_5 that has a high affinity for water and is used to remove moisture from a gas or another substance; a drying agent.

desiccate to remove (most of) the water from a substance or material containing moisture, especially with the aid of a **desiccant**; to dry. —**desiccation** *n.*

desiccator an apparatus in which to effect desiccation.

desmin *or (formerly)* **skeletin** a 50–55 kDa protein found in the Z disk of skeletal and cardiac muscle cells and in **intermediate filaments** in smooth muscle and non-muscle cells.

desmo+ *or (before a vowel)* **desm+** *comb. form* denoting ligament or bond.

desmofibrin a stabilized insoluble fibrin polymer formed from soluble fibrin polymer (*see* **fibrin**) in the final stage of **blood coagulation** by the action of factor XIII (fibrin-stabilizing factor) (*see* **blood coagulation**).

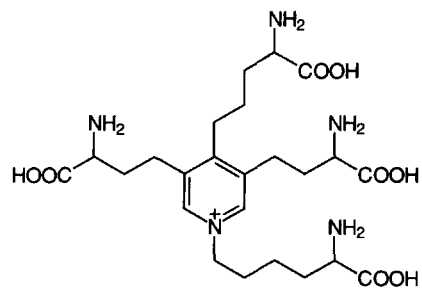
desmoglein a type I **membrane protein** of the mature desmosomal junction, involved in the interaction of plaque proteins and intermediate filaments mediating cell–cell adhesion. It contains **cadherin**-like repeats. Example (desmoglein 1 precursor) from human: database code DSG1_HUMAN, 1049 amino acids (113.59 kDa).

desmolase *former term for* any enzyme that catalyses the formation or rupture of a carbon–carbon bond.

desmoplakin any of several intracellular desmosome proteins that are probably involved in attaching intermediate filaments (e.g. keratin filaments in epithelial cells, desmin filaments in heart cells) to the desmosome. Example, desmoplakin I from human foreskin: database code HUMDPI, 2832 amino acids (327.35 kDa). *See also* **plakoglobin** (for desmoplakin III).

desmopressin 1-(3-mercaptopropanoic acid)-8-D-arginine vasopressin, desamino-[8-D-arginine]vasopressin; a synthetic analogue of **vasopressin** with greater antidiuretic activity and less pressor activity than the parent compound.

desmosine 4-(4-amino-4-carboxybutyl)-1-(5-amino-5-carboxypentyl)-3,5-bis(3-amino-3-carboxypropyl)pyridinium; a tetra(α-amino acid) isolated from hydrolysates of the fibrous protein **elastin**. Desmosine and **isodesmosine** covalently cross-link two or more polypeptide strands in this protein, the postulated mode of formation of both compounds being condensation of two residues of **allysine** in one polypeptide chain with one allysine and one lysine residue in a second polypeptide chain.



desmosome *or* **macula adherens** a patchlike intercellular junction found in vertebrate tissue. It consists of parallel zones of two cell membranes, separated by an interspace of 25–35 nm and having dense fibrillar plaques in the subjacent cytoplasm. The interspace is continuous with the intercellular space and contains a dense, central plaque of material rich in protein. These proteins are known as linker proteins and consist of cell–cell adhesion molecules of the **cadherin** type. Desmosomes are important in cell-to-cell adhesion and are particularly numerous in stratified squamous epithelium that is subject to mechanical stress. A similar type of intercellular junction, the **zona adherens**, sometimes also referred to as a desmosome, encircles the cell like a belt. —**desmosomal** *adj.*

desmotubule *see* **plasmodesma**.

desorb to remove adsorbed substances from a surface. —**desorption** *n.*; **desorbed** *adj.*

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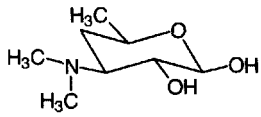
desosamine 3,4,6-trideoxy-3-(dimethylamino)-D-*xylo*-hexose; an aminodeoxy sugar component of several **macrolide** antibiotics, including **erythromycins** A, B, and C.



β-D anomer

desoxy+ *an obsolete variant of* **deoxy+**.

destain to remove dye in excess of that required to stain specifically the material in question, e.g. in staining proteins in an electrophoretogram. —**destaining** *n.*

destainer any apparatus used for removing excess dye electrophoretically from stained gels.

desthio+ *prefix* indicating the replacement of a sulfur atom by two hydrogen atoms.

destrin an **actin binding protein** similar to **cofilin** with wide tissue distribution. It severs actin filaments and binds to actin monomers. Example from pig: database code DEST_PIG, 165 amino acids (18.48 kDa).

Desulfovibrio a genus of Gram-negative, obligately anaerobic, asporogenous, chemotrophic bacteria that obtain energy by anaerobic respiration using reducible inorganic sulfur compounds.

detergent **1** a cleansing agent, especially a soap or (usually synthetic) soaplike substance that, when used in aqueous solution, cleanses by reducing surface tension. **2** having the properties of a detergent. *See also* **BigCHAP**, **Brij**, **C_xE_y**, **cetyltrimethylammonium bromide**, **CHAPS**, **CHAPSO**, **cholic acid**, ***n*-decyl-β-D-glucopyranoside**, ***n*-decyl-β-D-maltopyranoside**, **deoxyBigCHAP**, **deoxycholic acid**, **digitonin**, **dodecylglucopyranoside**, **dodecylmaltoside**, ***n*-dodecyl-*N*,*N*-dimethylglycine**, **Genapol**, **glycocholate**, **glycodeoxycholate**, **heptyl glucoside**, **heptyl thioglucoside**, **hexyl glucoside**, **lauryldimethylamine oxide**, **sodium dodecylsulfate**, **Lubrol**, **Mega-8**, **nonyl glucoside**, **NP-40**, **octyl glucoside**, **octyl thioglucoside**, **taurocholate**, **taurodeoxycholate**, **Triton**, **Tween**, **Zwittergent**.

detergent gel electrophoresis *an alternative name for* **SDS-polyacrylamide gel electrophoresis**.

deteriosome a microvesicle that is found in eukaryotic cells and is rich in phospholipase A_2 (*see* **phospholipase**). It is believed to represent a stage in membrane degradation.

detoxication *or (sometimes)* **detoxification**; the act or process of counteracting or rendering innocuous a poisonous substance. In an organism this involves various enzymic reactions by which harmful compounds, whether produced in the organism or introduced into it, are converted into (normally) less harmful substances and into more readily excretable products. Enzymic detoxication is brought about by chemical modification (frequently by oxidation) and/or conjugation with a normal metabolite. The enzymic process does not always result in a less toxic product and the term is sometimes restricted to those instances in which a less toxic product actually occurs, as distinct from **intoxication**. Enzymic detoxication may be divided into two phases. Phase 1 concerns metabolic transformation by a wide variety of oxidations, reductions, hydrolyses, etc., usually resulting in the introduction of functional groups that increase the polarity of the molecule and act as centres for phase 2 reactions. Phase 2 involves conjugation, in which the foreign compound itself or the compound resulting from phase 1 reactions is combined with endogenous substances, such as acetate, glucuronate, sulfate, or an amino acid, or is alkylated by introduction of methyl, or other groups, to form the more water-soluble ultimate excretory metabolite. *See also* **lethal synthesis**. —**detoxicate** *vb.*

detoxification **1** the removal of poison. **2** *(sometimes)* **detoxication**.

detoxify **1** to remove a poison or the effect of a poison. **2** to bring about **detoxication**.

deuterate to combine or label with **deuterium**. —**deuteration** *n.*; **deuterated** *adj.*

deuterium *symbol*: ^2H *or (deprecated)* D; a stable isotope of hydrogen, relative atomic mass 2.014, sometimes known as heavy hydrogen. Its relative abundance in natural hydrogen is 0.015 atom percent. It was much used as a tracer in studies of the chemistry and biochemistry of compounds containing non-labile hydrogen before the ready availability of tritium and carbon-14; its use continues in tracer experiments with detection by NMR spectroscopy, and where the use of radioactive compounds is contra-indicated. *See also* **heavy water**, **protium**, **tritium**.

deuterium (discharge) lamp a **hydrogen (discharge) lamp** filled with dideuterium in place of dihydrogen; this substitution increases the intensity 3- to 5-fold for the same power consumption and extends the upper limit of the continuum further into the visible range.

deutero+ *or (before a vowel)* **deuter+** *comb. form* **1** denoting that an indicated chemical compound or class of compound contains deuterium. **2** denoting second or secondary.

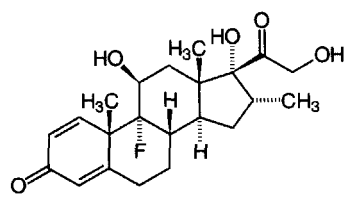
deuteron **1** *symbol*: $^2H^+$; the cation derived from an atom of deuterium. *Compare* **hydron**. **2** *symbol*: d; a particle of nucleon number two, having a charge equal and opposite to that of an **electron** and having a mass of 2.0136 dalton.

develop **1** to process an exposed photographic film with a **developer** in order to render the image visible. **2** to render visible the colourless substances on a chromatogram or electrophoretogram by treatment with a stain or chromogenic reagent. **3** to cause a solvent to flow through a chromatographic support in order to separate the components of an applied mixture. **4** *(of a cell, organ, or organism)* to undergo or cause to undergo a series of orderly changes whereby a mature state is attained. —**development** *n.*

developer **1** a solution of a reducing agent that renders visible the latent image on an exposed photographic film or paper by reducing to metallic silver those areas of silver halide that had been exposed to light. **2** a solution of a stain or chromogenic reagent used to render visible the colourless substances on a chromatogram or electrophoretogram.

Dewar flask *or* **Dewar** a double-walled vessel or flask, usually of silvered glass but sometimes of metal, in which the space between the walls is evacuated to prevent conduction and convection of heat between the inner and outer walls. It is used to maintain the contents at temperatures either higher or lower than that of the environment. [After its inventor Sir James Dewar (1842–1923), British chemist and physicist.]

dexamethasone 9*α*-fluoro-16*α*-methylprednisolone; a synthetic **glucocorticoid** with negligible mineralocorticoid activity that has actions similar to adrenal corticosteroids.



dextr+ *see* **dextro+**.

dextran any glucan of very high relative molecular mass and consisting of linear chains of *α*(1→6)-linked D-glucose residues, often with *α*(1→2)- or *α*(1→3)-branches. Native dextran, produced by a number of species of bacteria of the family Lactobacilliaceae, is a polydisperse mixture of components

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of M_r $<10^3$ to $>10^7$. Specific fractions of (partially hydrolysed) native dextran that have a narrow and well-defined size distribution may be designated by a numeric suffix equal to 10^{-3} × mass-average molar mass; e.g. Dextran T 500. Dextrans used in medicine are acid-degraded native dextrans.

dextranosome a **lysosome** loaded with dextran. It has higher than normal density.

dextransucrase EC 2.4.1.5; *systematic name*: sucrose:1,6-α-D-glucan 6-α-D-glucosyltransferase; *other name*: sucrose 6-glucosyltransferase. An extracellular bacterial enzyme that catalyses the reaction:

$$\text{sucrose} + (1,6\text{-}\alpha\text{-D-glucosyl})_n = \text{D-fructose} + (1,6\text{-}\alpha\text{-D-glucosyl})_{n+1}.$$

Streptococcus mutans dextransucrases are of several types: dextransucrase S produces water-soluble glucans (α(1→6)-linked glucose); dextransucrase I produces water-insoluble glucans (α(1→3)-linked glucose and some α(1→6)-linkages); and dextransucrase SI produces both types; the sequences are related. Example dextransucrase SI precursor from *S. mutans*: database code GTFC_STRMU, 1375 amino-acid residues (152.85 kDa); the first 24 residues are the signal. *See also* **sucrase** (def. 3).

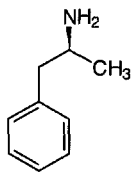
dextrin any of the poly-D-glucosides of intermediate chain length that are formed during the hydrolytic degradation of starch or glycogen by enzymes, acid, or heat. *See also* **limit dextrin**, **Schardinger dextrin**.

α-dextrin endo-1,6-α-glucosidase EC 3.2.1.41; *other names*: pullulanase; pullulan 6-glucanohydrolase; limit dextrinase; debranching enzyme; amylopectin 6-glucanohydrolase; the starch-debranching enzyme, which hydrolyses (1→6)-α-D-glucosidic linkages in pullulan and starch to form maltotriose. Example from *Klebsiella pneumoniae*: database code PULA_KLEPN, 1090 amino acids (117.97 kDa).

dextro- *symbol*: *d*-; a prefix, no longer used, to denote a compound that is **dextrorotatory**; the dextrorotatory enantiomer of compound A is now designated as (+)-A.

dextro+ *or (before a vowel)* **dextr+** *comb. form* denoting on or towards the right. *Compare* **levo+**.

dextroamphetamine (*S*)-methylbenzeneethanamine; the potent (–)-stereoisomer of **amphetamine**. One proprietary name is Dexamphetamine.



dextrorotatory *or (US)* **dextrorotary** **1** *symbol*: (+)- *or (formerly) d*-; describing a chemical compound that rotates the plane of polarization of a transmitted beam of plane-polarized light to the right, i.e. in a clockwise direction as viewed by an observer looking toward the light source. **2** describing any rightwards or clockwise rotation. *Compare* **levorotatory**. —**dextrorotation** *n.*

dextrorphan *see* **levorphanol**.

dextrose *traditional name (still used in pharmacy)* for D-glucose, D-(+)-glucopyranose, the dextrorotatory component of **invert sugar**. *Compare* **levulose**.

DFP *abbr. for* diisopropyl fluorophosphate.

dG *symbol for* a residue of the deoxynucleoside deoxyguanosine (alternative to dGuo).

dGMP *abbr. for* deoxyguanosine monophosphate, the common name for 2′-deoxyguanosine 5′-phosphate; 2′-deoxy-5′-guanylic acid; guanine 2′-deoxyriboside 5′-phosphate.

dGuo *symbol for* a residue of the deoxynucleoside deoxyguanosine; 2′-deoxyribosylguanine; guanine 2′-deoxyriboside (alternative to dG).

dGuo5′*P* *symbol for* deoxyguanosine 5′-phosphate.

dGTP *abbr. for* deoxyguanosine triphosphate, the common name for 2′-deoxyguanosine 5′-triphosphate, 2′-deoxy-5′-guanylyl diphosphate, guanine 2′-deoxyriboside 5′-triphosphate.

DH+ *abbr. for* dehydro+ *or* dihydro+ *or* dihydroxy+, sometimes prefixed to chemical names or alternatives. Its use is deprecated.

DHAS *abbr. for trans*-dehydroandrosterone, i.e. **dehydroepiandrosterone**.

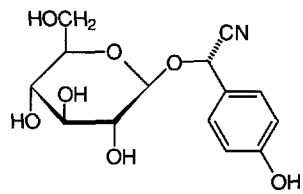
DHEA *abbr. for* dehydroepiandrosterone.

DHFR *abbr. for* dihydrofolate reductase.

DHPR *abbr. for* dihydropteridine reductase.

DHU arm *abbr. for* dihydrouridine arm of transfer RNA.

dhurrin L-*p*-hydroxymandelonitrile-β-D-glucopyranoside; a glucoside from the fruit of young *Sorghum vulgare*. *See also* **amygdalin**.



di+ *comb. form* **1** *(in chemical nomenclature) (distinguish from* **bis+** (def. 2)) **a** indicating the presence in a molecule of two identical unsubstituted groups, e.g. diethylsulfide, 1,3-dihydroxyacetone. **b** indicating the presence in a molecule of two identical inorganic oxoacid residues in anhydride linkage, e.g. adenosine 5′-diphosphate. **2** *or* **bis+** (def. 1) denoting two, twofold, twice, doubled.

diabetes any clinical condition characterized by thirst and the passing of large volumes of dilute urine, especially **diabetes mellitus**. *See also* **diabetes insipidus**. —**diabetic** *adj., n.*

diabetes-associated peptide *abbr.*: DAP; *another name for* **amylin**.

diabetes insipidus a disease characterized by thirst and the excretion of large volumes of hypotonic (dilute) urine, caused by any lesion, nervous or endocrine, that interferes with the normal secretion of **vasopressin** by the posterior pituitary gland. *See also* **nephrogenic diabetes insipidus**.

diabetes mellitus *or* (commonly) **diabetes** a disorder in which the level of blood glucose is persistently above the normal range. Two main forms of the disease are generally recognized. **Type 1 diabetes mellitus**, the so-called juvenile type, often manifests itself in children and young adults. There is a marked failure to release **insulin** from the B cells of the **islets of Langerhans** in the pancreas, and frequently an almost complete absence of insulin in the B cells. The only effective treatment is administration of insulin, hence the frequent designation of this form as **insulin-dependent diabetes mellitus** (*abbr.*: IDDM). Type 1 diabetes mellitus is thought to arise in many patients from autoimmune attack on the B cells. Without insulin a severe **ketoacidosis** rapidly develops, with tissue wasting resulting from breakdown of muscle protein and hydrolysis of triacylglycerols in fat depots. **Type 2 diabetes mellitus** or **maturity onset diabetes** tends to manifest itself in adults, especially if obese, though the distinction between types 1 and 2 is blurred. In type 2 there may often be secretion of significant amounts of insulin, but for reasons not well understood these are not fully effective. There is by definition a failure to lower blood glucose adequately after a **glucose tolerance test**; patients of this type seldom develop severe ketoacidosis. **Tolbutamide** and re-

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lated sulfonylureas can be used to stimulate insulin release in type 2. In both types of diabetes mellitus there may develop serious complications, including neuropathy, retinopathy, atherosclerosis, peripheral vascular disease, and nephropathy. Type 2 diabetes mellitus is also referred to as **non-insulin-dependent diabetes**.

diabetes mutation a mutation first identified in mice that spontaneously develop diabetic symptoms. It appears to be a mutation in the **leptin receptor** gene.

diabetic a sufferer from diabetes.

diabetogenic causing or being caused by **diabetes**.

diabetogenic hormone *former term for* **somatotropin**.

diabolic a term suggested to categorize enzymes that appear to serve a complex or multiple metabolic function. *See also* **amphibolic**.

diacetylchitobiose 4-*O*-(2-acetamido-2-deoxy-*β*-D-glucopyranosyl)-2-acetamido-2-deoxy-D-glucose; the repeating unit of **chitin**. *See also* **chitobiose**.

diacetylmorphine *other names*: diamorphine, heroin; a semisynthetic narcotic analgesic derived from **morphine** by acetylation and used either as the free base or its hydrochloride. It has more potent analgesic activity than the parent compound but otherwise its actions are similar. Noted for its dependence-inducing actions and potential for abuse, it is a controlled substance under the US Code of Federal Regulations; import and manufacture of diacetylmorphine and its salts are forbidden in the USA and other countries. *See also* **codeine**.

diacylglycerol *or (formerly)* **diglyceride** any (1,2- or 1,3-) diester of glycerol and two fatty acids; the latter may be identical or different.

diacylglycerol *O*-acyltransferase EC 2.3.1.20; *other name*: diglyceride acyltransferase; an enzyme that catalyses the synthesis of triacylglycerol from acyl-CoA and 1,2-diacylglycerol with release of CoA.

diacylglycerol cholinephosphotransferase EC 2.7.8.2; *other names*: phosphorylcholine–glyceride transferase; alkylacylglycerol cholinephosphotransferase; 1-alkyl-2-acetylglycerol cholinephosphotransferase; an enzyme of the pathway for the *de novo* synthesis of phosphatidylcholines. It catalyses the formation of a phosphatidylcholine from CDPcholine and 1,2-diacylglycerol with release of CMP. Example from yeast: database code CPT1_YEAST, 407 amino acids (46.25 kDa).

diacylglycerol kinase *abbr.*: DGK; EC 2.7.1.107; *systematic name*: ATP:1,2-diacylglycerol 3-phosphotransferase; *other name*: diglyceride kinase. An enzyme that catalyses the reaction between ATP and 1,2-diacylglycerol to form ADP and 1,2-diacyl-*sn*-glycerol 3-phosphate (phosphatidic acid). It plays an important part in the response of cells to agonists that stimulate the **phosphatidylinositol cycle**, being involved in the resynthesis of inositolphospholipids. The enzyme is stimulated by Ca^{2+} and phosphorylated by protein kinase C; it is an **EF-hand** protein. Example from human: database code KDGL_HUMAN: 735 amino acids (82.49 kDa).

diacytosis the process of transporting material across a cell, especially an epithelial cell, by **pinocytosis** at one surface, movement of the **pinocytic vesicle** across the cell, and **exocytosis** of its contents at another part of the cell surface.

diafiltration the process of separating microsolutes, e.g. salts, from a solution of larger molecules (or of exchanging them for different microsolutes) by **ultrafiltration** with continuous addition of solvent (or of a solution of the new microsolutes). This rapidly removes the original microsolutes from the solution, whose volume remains constant.

diagonal chromatography a two-dimensional chromatographic technique used to determine the sensitivity of a constituent of a mixture to some (photo)chemical process, e.g. oxidation. The sample is chromatographed in one direction, the process carried out *in situ*, and the specimen is then rechromatographed at right angles. Compounds unmodified by the treatment all lie on a diagonal line across the chromatogram.

diagonal electrophoresis a two-dimensional electrophoretic technique for determining the position of disulfide bonds in a polypeptide. The polypeptide is partially hydrolysed and the resulting smaller peptides separated by paper electrophoresis in one direction. After treatment on the paper with performic acid vapour, they are subjected to a second electrophoresis step at right angles. Those peptides not falling on a diagonal line on the paper contain cysteic acid residues formed by the oxidation of disulfide groups.

diakinesis the final phase of prophase I in **meiosis**.

dialdose any monosaccharide derivative containing two (potential) aldehydic carbonyl groups. *Compare* **aldose**, **diketose**.

diallyltartardiamide *abbr.*: DATD; *N*,*N*′-diallyl-L-tartramide, $[CH(OH)–CO–NH–CH_2–CH=CH_2]_2$; a compound sometimes used as a cross-linking agent in the preparation of polyacrylamide gels for electrophoresis or related separative procedures. Its structure contains a 1,2-diol grouping, which is susceptible to **periodate oxidation**. Such gels may thereby be solubilized after use to facilitate recovery of separated substances.

dialysable *or (esp. US)* **dialyzable** capable of being purified or separated by **dialysis**. The term has been used also, variously, to describe material that either can or cannot traverse a dialysis membrane. Some authorities prefer the term **diffusible** for material that can traverse a dialysis membrane. *See also* **dialysate**.

dialysate *or (esp. US)* **dialyzate** the solution resulting from **dialysis** that is free from colloidal material, i.e. free from material unable to pass through a dialysis membrane; the opposite of **retentate**. In the past the term has been used confusingly to describe both the material retained by the membrane and the material that has passed through a membrane. Some authorities prefer the term **diffusate** for the resulting colloid-free material and the term **analysis residue** for the retentate. *See also* **dialysable**.

dialyser *or (esp. US)* **dialyzer** an apparatus consisting of two or more compartments separated by **dialysis membrane(s)**, in which to carry out **dialysis**.

dialysis a process in which solute molecules are exchanged between two liquids through a membrane in response to differences in chemical potentials between the liquids. It is used especially for separating macromolecules (colloids) in solution from smaller dissolved substances (crystalloids) by selective ***diffusion*** through a ***semipermeable membrane***, which allows the passage of all components of the system except the macromolecules. *See also* **diafiltration**, **diasolysis**, **electrodecantation**, **electrodialysis**, **equilibrium dialysis**, **reverse dialysis**, **thin-film dialysis**, **ultrafiltration**. [From Greek *dialusis*, a separation or dissolution.] —**dialyse** *or (esp. US)* **dialyze** *vb.*; **dialytic** *adj.*; **dialytically** *adv.*

dialysis bag the significant component of a simple **dialyser**, commonly made from a convenient length of **dialysis tubing** by knotting or tying off one or both ends. When filled with the colloidal solution to be dialysed it is immersed or suspended in an appropriate colloid-free aqueous medium.

dialysis cell any small device for use as a **dialyser**.

dialysis membrane any semipermeable membrane suitable for **dialysis**, often made of cellulose acetate, cellulose nitrate, or regenerated cellulose. It may be fashioned into flat sheets or into continuous tubing. Most dialysis membranes are permeable to molecules of up to 12–14 kDa.

dialysis residue *an alternative name for* **retentate**.

dialysis tubing seamless tubular **dialysis membrane**.

diamagnetic pair a diamagnetic dimer produced by spin coupling of two paramagnetic (molecular or atomic) species.

diamagnetism the property displayed by substances that have a very small negative magnetic susceptibility, due to the changes induced in the orbital motions of atomic electrons by an applied external magnetic field; such changes generate a magnetic field in opposition to the applied field. Whereas such a phenomenon occurs in all substances it is often masked by

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the opposing and stronger effects of **ferromagnetism** or **paramagnetism**. —**diamagnetic** *adj.*

diamine any compound containing two amino groups or substituted amino groups.

diamine oxidase *see* **amine oxidase (copper-containing)**.

diamino+ *prefix (in chemical nomenclature)* indicating the presence of two (unsubstituted or substituted) amino groups.

diamino acid any organic acid, usually an alkanoic acid, that contains two (unsubstituted or substituted) amino groups.

di(α-amino acid) any compound whose molecules may be derived from two (identical or differing) molecules of α-aminoalkanoic acid however they are linked. The term includes (but is not limited to) any dipeptide.

diaminobenzoic acid *abbr.*: DABA; 3,5-diaminobenzoic acid; a compound that gives fluorescent products when heated in mineral acid solution with aldehydes. It is used for the microfluorimetric determination of DNA (as it does not react with RNA) and in the analysis of sialic acid.

diaminobutyric acid *symbol*: A_2bu; *abbr.*: Dab; α,γ-diaminobutyric acid; 2,4-diaminobutanoic acid; a diamino acid not occurring in proteins. The L enantiomer is sometimes found replacing *meso*-diaminopimelic acid in peptidoglycan of bacterial cell walls and several residues per molecule are present in the peptide antibiotics of the polymyxin group (together with one residue of the D enantiomer in polymyxin B_1). It also occurs in higher plants as a nonprotein amino acid.

diaminocaproic acid *see* **lysine**.

2,7-diaminofluorene a dye used in the chromogenic assay of peroxidases. It replaces benzidine, which was formerly used but is now known to be carcinogenic.

diaminopimelic acid *symbol*: A_2pm *or* Dpm; *abbr.*: DAP; α,ε-diaminopimelic acid, 2,6-diaminoheptanedioic acid; a α,ε-diaminodicarboxylic acid with two chiral centres. *meso*-Diaminopimelic acid is the stereoisomer occurring in peptidoglycan in the cell walls of *Escherichia coli* and all other Gram-negative bacteria. *See also* **diaminopimelic-acid pathway**.

diaminopimelic-acid pathway *or* **DAP pathway** a metabolic pathway for the synthesis of L-lysine from L-aspartic acid via α,ε-diaminopimelate. Found in bacteria, some lower fungi, and green plants, it involves an initial condensation between pyruvate and aspart-4-al, yielding, following dehydration, 2,3-dihydropicolinate. This substance is then reduced; ring opening occurs followed by succinylation to form α-(succinylamino)-ε-oxo-L-aminopimelic acid. Transamination, deacylation, and epimerization yield the corresponding *meso*-α,ε-diaminopimelic acid; then decarboxylation completes the overall synthesis of L-lysine. *Compare* **aminoadipic pathway**.

diamorphine *see* **diacetylmorphine**.

diaphorase *name formerly applied indiscriminately to* any enzyme capable of catalysing the oxidation of either NADH or NADPH in the presence of an electron acceptor such as a dye (e.g. Methylene Blue, or 2,6-dichlorophenolindophenol), ferricyanide, a quinone, or a cytochrome but not dioxygen. *Also formerly known as* **coenzyme factor**.

diaphragm **1** *(in chemistry)* a semipermeable membrane, or porous plate, used to separate two solutions in **dialysis** or **osmosis**. **2** *(in anatomy)* any separating membrane, especially the thin, domed fibromuscular partition separating the thorax from the abdomen. Flattening of the diaphragm, accompanied by expansion of the rib cage, causes air to be sucked into the lungs. **3** *(in optics)* any device, sometimes adjustable (e.g. iris diaphragm), that can limit or vary the aperture of a lens or optical system. **4** any other thin dividing membrane.

diarylpropane peroxidase *see* **ligninase**.

diasolysis a membrane permeation process for the separation of organophilic from hydrophilic solutes, akin to **dialysis** but differing in that separation depends primarily on the relative solubilities of the solutes in the membrane rather than on their molecular dimensions. Such a process may play a part in the selective passage of solutes through membranes of living cells.

diastase **1** *obsolete name for* α-amylase (EC 3.2.1.1). **2** the crude mixture of amylases obtained commercially as a yellowish white amorphous powder from malt. [From Greek *diastasis*, a separation.] —**diastatic** *adj.*

diastatic activity the enzymic activity of α-amylase.

diastereoisomer *or* **diastereomer** any **stereoisomer** that is not **enantiomeric**; it may be either chiral or achiral. The term includes ***cis–trans* isomer**, **configurational isomer**, **conformational isomer**, and **epimer**. —**diastereoisomeric** *or* **diastereomeric** *adj.*; **diastereoisomerism** *or* **diastereomerism** *n.*

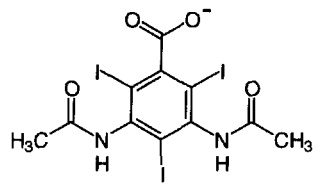
diastereotopic **1** chemically-like ligands in constitutionally equivalent locations that are not symmetry related (cannot be interchanged by rotation about an axis (C_n) or alternating axis (S_n) of symmetry) are diastereotopic; the two ligands are in a stereochemically different, nonmirror-image environment. Separate replacement of each ligand by a different achiral ligand yields two products that are in a diastereoisomeric relationship. Example: replacement of the H_R hydrogen of the methylene group in (*R*)–CH_3–CH_2–CHBr–CH_3 with chlorine yields (2*R*,3*R*)-2-bromo-3-chlorobutane; the similar replacement of the H_S hydrogen yields the diastereoisomeric (2*R*,3*S*)-2-bromo-3-chlorobutane. A biochemically important example is that both of the methylene groups of citric acid have diastereotopic hydrogens. **2** the two faces of a double bond or of a planar cyclic ring system that are not related by any symmetry operation (axis, plane, centre, or alternating axis) are diastereotopic; the two faces show stereochemically different, nonmirror-image environments. Separate addition of an achiral reagent to each face yields two diastereoisomeric products. Example: hydrogenation of the C=O bond in (3*S*)–CH_3–CH_2–$CH(CH_3)$–CO–COOH (in absence of any chiral influence such as a chiral catalyst) yields the two diastereoisomers, (2*R*,3*S*)-2-hydroxy-3-methylpentanoic acid and (2*S*,3*S*)-2-hydroxy-3-methylpentanoic acid. A biochemical example is the two diastereotopic faces, *A* and *B*, of the (dihydro)pyridine ring of nicotinamide-adenine coenzymes (*see* **nicotinamide-adenine dinucleotide (reduced)**). *Compare* **enantiotopic**.

diastole **1** the passive dilatation of the chambers of the heart that occurs between the rhythmical contractions. **2** the rhythmical expansion of a pulsating vacuole. *Compare* **systole**. —**diastolic** *adj.*

diatomaceous earth *or* **kieselguhr** a friable, whitish material consisting mostly of silica, derived from diatomite, a rock consisting largely of the remains of diatoms. It is used as a filter aid and as an absorbent in column chromatography. *See also* **Berkefeld filter**.

diatomic *(of a molecular entity)* composed of only two atoms. —**diatomicity** *n.*

diatrizoate the anion 3,5-diacetamido-2,4,6-triiodobenzoate. Its sodium salt forms solutions of low viscosity and high relative density. A mixture with Ficoll provides a solution having the optimal density and osmolarity for the rapid, one-step isolation of lymphocytes from small volumes of blood by centrifugation. It is also used as a radiopaque material.



diauxy the adaptation of microorganisms to culture media containing two different carbohydates. Growth occurs in two phases separated by a period of less rapid or zero growth. In the first phase, the organism utilizes the carbohydrate for which it possesses constitutive enzymes. During the interlude

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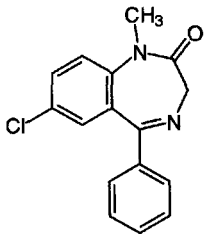
the organism synthesizes the required induced enzymes for the metabolism of the other carbohydrate, which it then proceeds to exploit in the second growth phase. —**diauxic** *adj.*

diazepam 7-chloro-1,3-dihydro-1-methyl-5-phenyl-2*H*-1,4-benzodiazepin-2-one; one of the most widely used **benzodiazepine** drugs, noted for its CNS depressant effects. Used as an anti-anxiety–hypnotic agent at subsedative doses, its actions are similar to those of chlordiazepoxide, but it has greater potency. One proprietary name is Valium.



diazepam binding inhibitor a 10 kDa 86-residue polypeptide, that acts as an endogenous ligand for a mitochondrial receptor (formerly regarded as a peripheral benzodiazepine binding site) in steroidogenic cells (i.e. adrenocortical, glial, and Leydig cells) and regulates stimulation of steroidogenesis by tropic hormones. It also binds to the benzodiazepine binding site on the $GABA_A$ receptor and modulates glucose-dependent insulin secretion and synthesis of acyl-CoA esters.

diazo compound any organic compound, other than an **azo compound**, that contains the bivalent **azo** group –N=N– (or $=N_2$) in covalent linkage. It may be (1) any aliphatic compound of general formula $R–CH=N_2$, in which both nitrogen atoms are linked to the same carbon atom by replacing two hydrogen atoms of the parent molecule, e.g. diazomethane, $CH_2=N_2$; or (2) any aromatic compound of general formula Ar–N=N–X in which one nitrogen atom is linked to a carbon atom of the aromatic ring by replacing one hydrogen atom of the parent molecule, and the other nitrogen atom is linked covalently to a group X through an atom other than carbon (except when X = CN), e.g. benzenediazohydroxide, $C_6H_5–N=N–OH$.

diazonium compound any aromatic organic compound of general formula $Ar–N_2^+$, containing the univalent cationic **diazonium group**, $–N^+\equiv N$, linked to a carbon atom of an aromatic ring system by replacing one hydrogen atom of the parent molecule. The positive charge is balanced by an anion to form a **diazonium salt**, e.g. benzenediazonium chloride, $C_6H_5–N_2^+Cl^–$.

diazotize *or* **diazotise** to cause a primary aromatic amine to form a **diazonium compound** by reaction with nitrous acid in the presence of a strong acid, according to the equation:

$$Ar\text{-}NH_2 + HONO + H^+ = Ar\text{-}N_2^+ + 2H_2O.$$

—**diazotized** *adj.*; **diazotization** *n.*

dibasic cleavage site a site within a proprotein structure at which endopeptidases act specifically to cleave the protein to one or more active polypeptides. It comprises a connected pair of basic amino-acid residues (Arg–Arg, Arg–Lys, Lys–Arg, or Lys–Lys). The cleavage is effected by a family of cellular endoproteases. These have catalytic domains related to **subtilisin** and go under the general name mammalian **prohormone convertases** (PCs). Examples are ***kex2***, first described in yeast, PC2 in human insulinoma, PC3, and **furin**. Dibasic cleavage sites occur e.g. in **proinsulin**, **proopiomelanocortin**, and **chromogranins**.

dibenzazepine any of a group of compounds with a tricyclic structure related to phenothiazines that prevent the neuronal reuptake of norepinephrine or 5-hydroxytryptamine from the synaptic cleft, and are useful as drugs in the treatment of depression, e.g. imipramine, clomipramine.

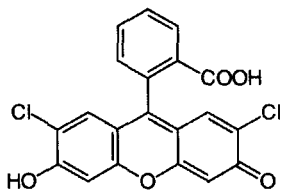
dibenzocycloheptene any of a group of agents that prevent neuronal reuptake of norepinephrine and 5-hydroxytryptamine from the synaptic cleft and are useful as drugs in the treatment of depression, e.g. amitriptyline.

dicarboxylate transport protein *former name for* **oxoglutarate/malate carrier protein.**

dicarboxylic acid any organic compound containing two carboxyl groups.

dicaryon *a variant spelling of* **dikaryon.**

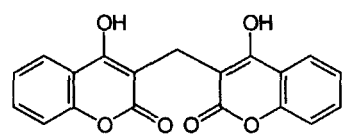
2′,7′-dichlorofluorescein a dye useful as a detection reagent for lipids, yielding fluorescent spots on chromatograms under UV light.



dichroic ratio the ratio of the absorbance of light polarized perpendicularly to the axis of a nonisotropic sample (e.g. the fibre axis of a protein or nucleic-acid molecule or one axis of a crystal) to the absorbance of light polarized parallel to the sample axis. If the dichroic ratio is greater than unity, the vibrational transition observed is said to exhibit **perpendicular dichroism**; if less than unity, it is said to show **parallel dichroism.**

dichroism **1** the directional effect observed in the absorption of electromagnetic radiation resulting from the relative orientations of the absorbing chromophore and the direction of the electric vector in the polarized electromagnetic radiation. Thus the absorption of such radiation may be restricted only to atoms or groups that vibrate in a specific direction or to a component of the radiation that is polarized in a specific direction. *See* **circular dichroism**, **dichroic ratio**, **electric dichroism.** **2** concentration- and path-length-dependent changes in the frequencies of electromagnetic radiation absorbed by solutions of certain substances. —**dichroic** *adj.*

dicoumarol *or* **dicumerol** *or (esp. US)* **dicumarol** (*formerly* bishydroxycoumarin); 3,3′-methylenebis(4-hydroxycoumarin), 3,3′-methylenebis(4-hydroxy-2*H*-1-benzopyran-2-one); a substance originally isolated from spoiled sweet clover but now synthetic, that prevents the normal formation of prothrombin and other blood coagulation factors. It interferes with the action of vitamin K in γ-carboxylation of certain glutamic residues in the precursors of the coagulation proteins. It is used therapeutically as an anticoagulant, and is also used as a rodenticide. **Warfarin** is one of the **coumarins.**



dicoumarol

dictyosome **1** *or* **golgiosome** *an alternative name for* **Golgi apparatus**, especially in cells of invertebrates and plants; there are usually several scattered dictyosomes per cell. **2** a collar-like

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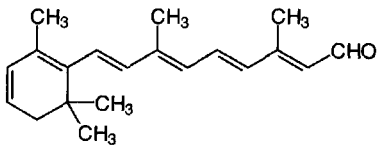
structure that may form an anchor for the base of the flagellum in uniflagellate fungi.

Dictyostelium discoideum a cellular **slime mould**. It exists in the vegetative form as unicellular, haploid **myxamoebae**, 8–12 μm maximum dimension, using bacteria as food. In the absence of bacteria, chemotactic aggregation of myxamoebae occurs, mediated by myxamoebal secretion of acrasin (i.e., cyclic AMP), to form an elongated, finger-like, multicellular **pseudoplasmodium**, 1–4 mm maximum dimension. Aggregation is assisted by the synthesis of a multivalent carbohydrate-binding lectin, **discoidin**, found in the outer membrane of starved cells. The pseudoplasmodium differentiates to form a single, unbranched stalk, the **sorocarp**, which carries a spheroidal or ovoid mass of yellow spores, each commonly 5–10 μm × 3–6 μm with a thick cellulose-containing wall. Germination of spores only occurs in the presence of an adequate supply of amino acids.

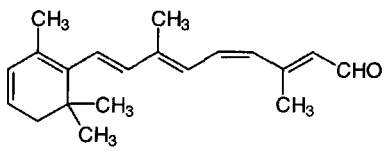
dicyclohexylcarbodiimide *see* **DCC**. *See also* **carbodiimide**.

didehydro+ *prefix (in chemical nomenclature)* denoting the loss of two hydrogen atoms. *See also* **dehydro+**.

3,4-didehydroretinal *recommended trivial name for* (3-)dehydroretinal; (3-)dehydroretinaldehyde; retinal$_2$; vitamin A_2 aldehyde; retinene$_2$; (2*E*,4*E*,6*E*,8*E*)-3,7-dimethyl-9-(2,6,6-trimethylcyclohex-1,3-dien-1-yl)nona-2,4,6,8-tetraen-1-al; the didehydro derivative of **retinal** (def. 2). This all-*E*-isomer, 3,4-didehydro-all-*trans*-retinal, often termed all-*trans*-retinal$_2$, plays a role in the visual process in freshwater fish and some amphibians analogous to that of all-*trans*-retinal in other vertebrates; *see* **retinal** (def. 2). Its isomerization product, the (2*E*,4*Z*,6*E*,8*E*)-stereoisomer, generally termed 11-*cis*-retinal$_2$, combines (as a **Schiff base**) with an opsin to form (in cone cells) **cyanopsin** or (in rod cells) **porphyropsin**. *Note*: The numbering system of the systematic name is different from that of the trivial name, the latter following the rules used for carotenoids.

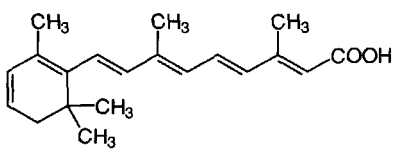


(all-*E*) isomer

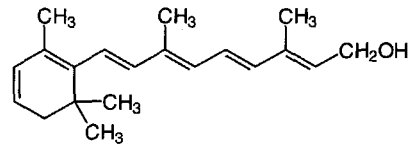


(2*E*,4*Z*,6*E*,8*E*) isomer

3,4-didehydroretinoic acid *recommended trivial name for* (3-)dehydroretinoic acid; vitamin A_2 acid; (2*E*,4*E*,6*E*,8*E*)-3,7-dimethyl-9-(2,6,6-trimethylcyclohex-1,3-dien-1-yl)nona-2,4,6,8-tetraenoic acid; the didehydro derivative of **retinoic acid**.

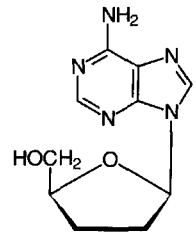


3,4-didehydroretinol *recommended trivial name for* (3-)dehydroretinol; retinol$_2$; vitamin A_2; vitamin A_2 alcohol; (2*E*,4*E*,6*E*,8*E*)-3,7-dimethyl-9-(2,6,6-trimethylcyclohex-1,3-dien-1-yl)nona-2,4,6,8-tetraen-1-ol; the didehydro derivative of **retinol**, being characterized by a second double bond in the terminal ring of the molecule. It is the predominant form of vitamin A in freshwater fishes. *See also* **vitamin A**.

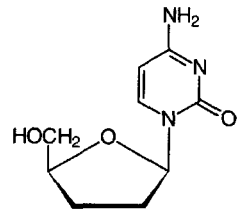


dideoxy+ *prefix (in organic chemical nomenclature)* **1** denoting the replacement of two hydroxyl groups by two hydrogen atoms. **2** (*abbr.*: dd+) indicating the presence in a nucleoside of a residue of 2,3-dideoxy-D-ribose.

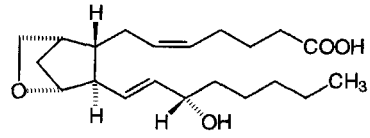
dideoxyadenosine *symbol*: ddAdo *or* ddA; *abbr.*: DDA; 2′,3′-dideoxyadenosine; an adenosine analogue with antiviral activity.



dideoxycytidine *symbol*: ddCyd *or* ddC; *abbr.*: DDC; 2′,3′-dideoxycytidine; a cytidine analogue with antiviral activity.



9,11-dideoxy-9α,11α-epoxymethanoprostaglandin $F_{2\alpha}$ U46619; a stable **thromboxane** A_2 mimetic.



dideoxyinosine *symbol*: ddIno *or* ddI; *abbr.*: DDI; 2′,3′-dideoxyinosine; an **inosine** analogue with antiviral activity.

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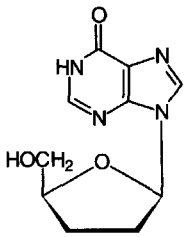
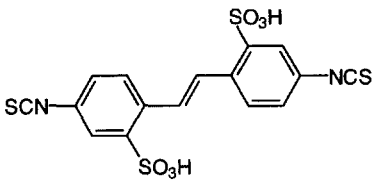


dideoxyinosine

dideoxy method *or* **dideoxy(nucleotide) sequencing analysis** *an alternative name for* **chain-termination method** (for sequencing DNA molecules).

dideoxynucleoside triphosphate *abbr.*: ddNTP; any artificial nucleoside triphosphate in which both of the hydroxyl groups on C-2′ and C-3′ of the pentose moiety have been replaced by hydrogen atoms. They are used in sequencing DNA molecules by the **chain-termination method**.

DIDS *abbr. for* 4,4′-diisothiocyano-2,2′-disulfonic acid stilbene; a powerful anion-transport inhibitor



didymium glass a glass with a bluish-pink coloration due to the inclusion of a mixture of rare-earth elements, chiefly neodymium and praseodymium. It has intense, narrow, light-absorption bands, and is used for calibrating spectrometers. An example is a glass known as Corning 5120, which has absorption bands at 441, 528.7, 585, 684.8, 743.5, 754, 808, 883, and 1067 nm.

dielectric **1** a substance or medium that can sustain an electric field but does not conduct electricity; an insulator. **2** of, relating to, or being a dielectric.

dielectric absorption the strong absorption of microwave electric fields shown by polar liquids, particularly water. It is especially troublesome in **electron spin resonance spectroscopy**.

dielectric constant *an obsolete term for* **relative permittivity**.

dielectric dispersion variation of the **relative permittivity** with the frequency of the applied electric field.

dielectric increment the change in the **relative permittivity** of a solution with the change in the concentration of the solute. For low concentrations of solute in polar solvents, the dielectric increment, $\delta D/\delta c$, is equal to $(D - D_0)/c$, where D and D_0 are the relative permittivities of the solution and solvent, respectively, and c is the solute concentration.

dielectrophoresis *the translational motion of neutral* suspended particles relative to that of the suspending medium when the suspension is subjected to a nonuniform electric field. The movement is the result of polarization induced in the particles, the degree of which is dependent on the ratio of the relative permittivities (*formerly* dielectric constants) of particles and medium. In **positive dielectrophoresis** (that most commonly observed), movement of the particles is towards the region of highest field intensity, irrespective of its sign (*compare* **electrophoresis**). **Negative dielectrophoresis** may be observed in certain frequencies when an alternating field is used, the particles then being attracted less than the medium to the region of most intense field; at such frequencies the polarizability of the particles is not greater than that of the medium. Dielectrophoresis is used, e.g., in the concentration of certain biological products, the characterization of single-celled organisms or cellular organelles by their characteristic yield spectrum (i.e. yield vs. field frequency), and the determination of the diffusion coefficients of proteins in solution.

diene any **alkadiene** or substituted alkadiene.

+diene(+) *or (before a vowel)* **+dien+** *(in chemical nomenclature) infix or suffix* in systematic names denoting the presence in a molecular structure of an unsaturated aliphatic hydrocarbon chain containing two (conjugated or unconjugated) double bonds. The position of each double bond may be indicated by a locant for its lowest-numbered carbon atom; e.g. cyclohexa-1,3-diene, eicosa-8,11-dienoic acid.

dienoic indicating a compound having an aliphatic chain with two double bonds and a carboxyl group.

dienoyl *general name for* any acyl group derived from an unsaturated fatty acid containing two (conjugated or unconjugated) double bonds.

2,4-dienoyl-CoA reductase (NADPH) EC 1.3.1.34; *systematic name*: *trans*-2,3-didehydroacyl-CoA:NADP$^+$ 4-oxidoreductase; *other name*: 4-enoyl-CoA reductase (NADPH). An enzyme of the pathway for oxidation of unsaturated fatty acids that catalyses the reduction by NADPH of *trans,trans*-2,3,4,5-tetradehydroacyl-CoA to *trans*-2,3-didehydroacyl-CoA, a normal substrate of β oxidation. For the bacterial enzyme, this is a direct product of the enzyme, but for the mammalian enzyme the product is *trans*-3,4-didehydroacyl-CoA, which must undergo isomerization to *trans*-2,3-didehydroacyl-CoA. Example from rat liver: database code RATDCR, 335 amino acids (36.16 kDa). *See also* **unsaturated fatty acid oxidation**.

diesterase *see* **phosphodiesterase**.

dietary deficiency a nutritional deficiency due to inadequate intake of one or more specific and necessary constituents of the diet, even though the diet may in other respects be adequate quantitatively.

diethyl ether *see* **ether**.

diethylstilbestrol *or (esp. UK)* **diethylstiboestrol** 4,4′-(1,2-diethyl-1,2-ethenediyl)bisphenol; a nonsteroidal compound that possesses the activity of an **estrogen**. It is used therapeutically to replace natural hormones, and was formerly used as a growth promoter in livestock (this use is now prohibited in many countries, including the UK and USA). It was originally used for the treatment of prostatic cancer.

difference spectrophotometry a spectrophotometric method for investigating the effects of potential perturbants on a chemical substance or system in solution. Two samples are prepared containing identical solutions except that one contains a potential perturbant, e.g. a protein denaturant. The absorbances of the two samples at each frequency are subtracted one from another generating a **difference spectrum** and thereby highlighting any small differences between the spectra of the normal and perturbed systems.

differential centrifugation centrifugation of a suspension in a succession of increasing gravitational fields so that particles of differing sizes and/or relative densities may be separated and collected.

differential counting counting of the pulses produced in a **scintillation counter** that fall within two or more differing energy ranges selected for with a pulse-height analyser. The technique is used for counting the disintegrations due to two or more radionuclides in the same sample.

differential labelling a method of determining the part of a molecule that reacts in a particular way by blocking one part with a specific reagent and investigating whether a particular reaction will still occur. It is used, e.g., for investigating the combining sites of antibodies.

differential medium any medium used for growing microorganisms that reveals specific properties of the organism(s)

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grown and hence aids in identification of the organism(s). *See also* **selective medium**.

differential scanning calorimetry *abbr.*: DSC; a form of **differential thermal analysis** in which the temperatures of both the sample and the reference substance are maintained at either the same or a constant difference; the amount of heat that must flow into the sample to maintain the temperature differential during a transition is then measured.

differential thermal analysis *abbr.*: DTA; a method for analysing temperature-induced transitions in a sample. The sample and an inert reference material are heated or cooled at the same rate and the difference in temperature between them is monitored. This difference is zero or constant until a thermally induced transition occurs in the sample, when the temperature difference changes. The direction of the change shows whether the transition is endo- or exothermic.

differential titration the titration of a group, e.g. an acid group, before and after another group in the same molecule has reacted with some other reagent. It is used to determine the extent, if any, of **linkage** between the functions of the groups in question. *See* **titrate**.

differentiating-stimulating factor *see* **leukemia inhibitory factor**.

differentiation the process whereby relatively unspecialized cells, e.g. embryonic or regenerative cells, acquire specialized structural and/or functional features that characterize the cells, tissues, or organs of the mature organism or some other relatively stable phase of the organism's life history.

differentiation antigen any cell-surface antigen whose expression varies during successive developmental stages of a particular cell type.

diffraction the bending of light, or other waves, by an obstacle or aperture, into the region of the geometrical shadow of the object; any redistribution in space of the intensity of waves resulting from the presence of an object in their path causing variations of either their amplitude or their phase. The effect is particularly marked when the size of the object is of the same order as that of the wavelength of the waves. Diffraction accounts for the phenomenon observed when light passes through an aperture and falls on a screen; this takes the form of patterns of light and dark bands (with monochromatic light) or coloured bands (with heterochromatic light) near the edges of the beam and extending into the shadow. Diffraction is also responsible for the propagation of radio waves over the surface of the globe and of sound waves around solid objects. *See* **diffraction grating**, **electron diffraction**, **X-ray diffraction**.

diffraction grating a glass or quartz plate on the surface of which there is a large number of equidistant parallel black lines (500 or more per millimetre). When light or other electromagnetic radiation passes through such a grating it is diffracted in a manner dependent on the wavelength of the radiation. Other plane surfaces, e.g. metals, may be used.

diffusate a product of a process of diffusion, especially the material that enters into or traverses a barrier of restricted or selective permeability. In **dialysis** the term is sometimes preferred to **dialysate**. *Compare* **nondiffusible material**.

diffusible **1** capable of diffusing. **2** *(sometimes) a preferred alternative term for* **dialysable** (i.e. capable of passing through a semipermeable membrane used in dialysis).

diffusion **1** the net flow of molecules from a region of high concentration, or high chemical potential, to one of low concentration, or low chemical potential, due only to random thermal motion. *See also* **facilitated diffusion**. **2** the irregular reflection or transmission of light or other electromagnetic radiation; scattering. **3** the act or process of dispersing or of being dispersed widely. —**diffuse** *vb., adj.*

diffusion cell *or* **diffusion chamber** **1** a cell or chamber with porous walls that allow the passage of dissolved substances but not of biological cells. It is used in studying materials released by cells. **2** a device for measuring the diffusion of macromolecules and consisting of two chambers separated by a porous membrane of nearly parallel channels. The channels are large compared with the size of the macromolecules but small enough that the bulk flow of liquid through them is negligible.

diffusion coefficient *or* **diffusion constant** *symbol*: *D*; a coefficient of proportionality between flux and concentration gradient for a solute diffusing in a system of constant temperature and pressure in accordance with **Fick's first diffusion law** and **Fick's second diffusion law**. For an ideal solute it is a constant, but in practice usually varies with concentration. The cgs unit for *D* is $cm^2\,s^{-1}$ (*see also* **Fick unit**) and the SI unit is $m^2\,s^{-1}$.

diffusion-controlled *or* **diffusion-limited** describing a chemical reaction (or other process) whose velocity is dependent on the rate at which one or all of the reactants (or participants) can diffuse to the site at which the reaction (or process) occurs, as to the active site of an enzyme catalysing the reaction.

diffusion gradient any gradient e.g. in the concentration of a dissolved solute that forms if the solute is capable of diffusing from a region of higher concentration to a region of lower concentration until its concentration in the solution is uniform.

diffusion-limited *see* **diffusion-controlled**.

diffusion potential an electric potential difference across a membrane due to the diffusion through the membrane of more cationic charges than anionic charges, or vice versa.

diffusive characterized by diffusion. —**diffusively** *adv.*

DIFP *see* **DFP**.

digest **1** to subject material to enzymic or chemical breakdown. **2** to subject food to **digestion** (def. 1). **3** to break down nitrogenous compounds by hot sulfuric acid to convert them to ammonium salts. **4** to treat biological materials with powerful oxidants to facilitate determination of trace elements present. **5** the mixture of compounds obtained from the enzymic or chemical degradation of a macromolecule or other substance. —**digester** *n.* an apparatus that facilitates digestion procedures.

digestion **1** the whole of the physical, chemical, and biochemical processes carried out by living organisms to break down ingested nutrients into components that may be easily absorbed and directed into metabolism. **2** the process of breaking down complex substances or materials into smaller parts either enzymically or chemically, especially in the course of their analysis.

digestive enzyme any hydrolytic enzyme that brings about or assists in **digestion** (def. 1).

digestive juice any of the secretions entering the digestive tract that contain digestive enzymes. They include saliva, **gastric juice**, **intestinal juice**, and **pancreatic juice**.

digestive system the digestive tract together with related organs, such as the pancreas and liver.

digestive tract *or* **alimentary tract** the tubelike passage in higher animals, extending from the mouth to the anus, in which the food is digested, from which absorption of nutrients occurs, and which serves to eliminate waste products.

diginose the D enantiomer, 2,6-dideoxy-3-*O*-methyl-D-*lyxo*-hexose, is a component of some **cardiac glycosides**

digitalis **1** any plant of the genus *Digitalis*. **2** a preparation of powdered dried leaves of the purple foxglove (*Digitalis purpurea*). It contains the cardiac glycosides **digitoxin**, **gitoxin** (a glycoside of 3,14,16-trihydroxycard-20(22)-enolide), and **gitaloxin** (16-formylgitoxin), and is used therapeutically to increase the strength of the heart's contraction and to slow auricular–ventricular conduction.

digitalose the D enantiomer, 3-methyl-D-fucose, 6-deoxy-3-*O*-methyl-D-galactose, is a component of some **cardiac glycosides**, e.g. digitoxin.

digitogenin (25*R*)-5α-spirostan-2α,3β,15β-triol; the aglycon of the glycosides (saponins) present in **digitonin**.

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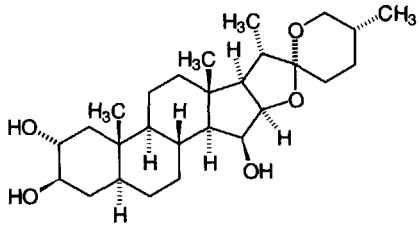
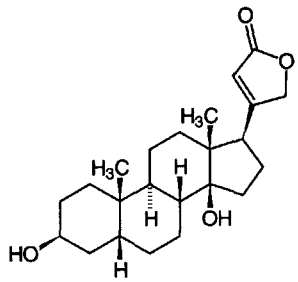


digitogenin

digitonin a mixture of at least four steroid saponins obtained from the seeds of the purple foxglove, *Digitalis purpurea*. It is useful in the fractional precipitation and analysis of cholesterol and other steroids and as a nonionic detergent in the solubilization of membrane proteins. Aggregation number 60. Its aglycon is **digitogenin**.

digitoxigenin 3β,14-dihydroxy-5β-card-20(22)-enolide; the aglycon of **digitoxin**.

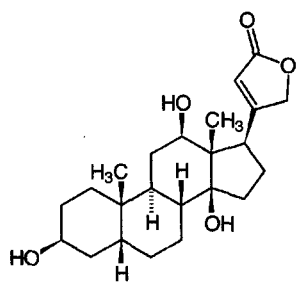


digitoxin a secondary glycoside, or mixture of glycosides comprised mainly of digitoxin, that is extracted from *Digitalis purpurea*. It has actions similar to, but longer-lasting than, **digoxin**. Its aglycon is digitoxigenin. *See also* **cardiac glycoside**.

digitoxose the D enantiomer, 2,6-dideoxy-D-*ribo*-hexose, is a component of some **cardiac glycosides**.

diglyceride *former name for* **diacylglycerol** (it is still quite commonly used, as in 'diglyceride fraction', but its use is discouraged for such purposes as diglyceride is properly a generic term for any compound having two glyceryl residues, e.g. **phosphatidylglycerol**).

digoxigenin 3β,12β,14-trihydroxy-5β-card-20(22)-enolide; the aglycon of **digoxin**.



digoxin a secondary glycoside extracted from the Austrian (or woolly) foxglove, *Digitalis lanata*. It acts on the heart to potentiate contractility and reduce conductivity mainly through inhibition of Na^+,K^+-ATPase, hence its use in congestive heart failure and atrial dysrhythmia. Its aglycon is digoxigenin. *See also* **cardiac glycoside**.

dihedral having or contained by two planes or plane faces.

dihedral angle the inclination of two planes that meet at an edge.

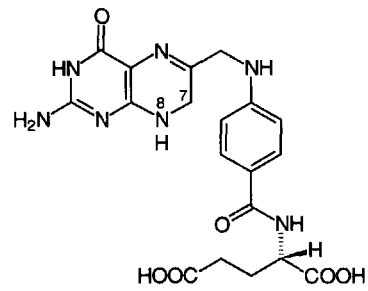
dihedral symmetry the symmetry of a **point group**, designated D_n, containing an n-fold axis with n twofold axes perpendicular to it.

dihomo-(6,9,12)-linolenate dihomogammalinolenate, dihomo-γ-linolenate, (*all-Z*)-eicosa-8,11,14-trienoate; an intermediate in the synthesis of arachidonate from linoleate, formed by Δ^6 desaturation and chain elongation. It acts as a precursor for the PG_1 series of **prostaglandins**. *See also* **eicosatrienoic acid**.

dihydric describing a chemical compound containing two hydroxyl groups per molecule. It is used especially of **alcohols**. *Compare* **dihydroxy+**.

dihydro+ *prefix (in chemical nomenclature)* indicating the presence of two additional hydrogen atoms.

dihydrofolate *abbr.*: H_2folate (DHF not recommended); **1** 7,8-dihydrofolate, 7,8-dihydropteroylglutamate; *the trivial name for* the 7,8-dihydro derivative of **folate** (def. 1). **2** any **folate** (def. 2) that is a dihydro compound, especially any of the respective 7,8-dihydro intermediates in the conversion of non-reduced folates to their corresponding folate coenzymes (i.e. tetrahydrofolates) by the enzyme dihydrofolate reductase. *See also* **antifolate**, **tetrahydrofolate**.



dihydrofolate reductase *abbr.*: DHFR; EC 1.5.1.3; *systematic name*: 5,6,7,8-tetrahydrofolate:$NADP^+$ oxidoreductase; *other name*: tetrahydrofolate dehydrogenase. An enzyme that catalyses the interconversion of 5,6,7,8-tetrahydrofolate and 7,8-dihydrofolate, and also slowly interconverts 7,8-dihydrofolate and folate; both reactions are linked to the reduction/oxidation of $NADP^+$/NADPH. It is inhibited by **aminopterin**, amethopterin (*also termed* **methotrexate**), and **trimethoprim**. Example from human: database code NRL_1DRF, 186 amino acids (21.30 kDa); 3-D structure known; four motifs.

dihydrofolate synthase EC 6.3.2.12; *other name*: dihydrofolate synthetase; an enzyme of the pathway for the *de novo* synthesis of dihydrofolate. It catalyses the formation of dihydrofolate from ATP, dihydropterate, and L-glutamate with release of ADP and orthophosphate. Example from *Escherichia coli*: database code FOLC_ECOLI, 422 amino acids (45.39 kDa).

dihydrogen *systematic name for* the diatomic compound H_2, commonly termed (molecular) hydrogen.

dihydrolipoamide S-acetyltransferase EC 2.3.1.12; *other names*: lipoate acetyltransferase; thioltransacetylase A; an enzyme that catalyses the formation of acetyl-CoA and dihydrolipoamide from *S*-acetyldihydrolipoamide and CoA. A lipoyl group is required as a coenzyme, the enzyme having three covalently linked lipoyl groups. This is the E_2 component of the **pyruvate dehydrogenase complex**. Example: dihydro-

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lipoamide acetyltransferase component (E_2) of a human pyruvate dehydrogenase complex precursor (PDC-E_2): (incomplete sequence) ODP2_HUMAN, 615 amino acids (65.32 kDa).

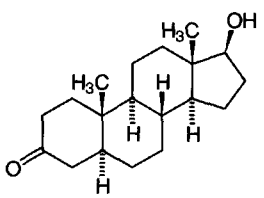
dihydrolipoamide dehydrogenase EC 1.8.1.4; *other names*: lipoamide reductase (NADH); lipoyl dehydrogenase; dihydrolipoyl dehydrogenase; diaphorase; the E_3 component of α-ketoacid dehydrogenase complexes, an FAD-flavoprotein enzyme that catalyses the oxidation by NAD^+ of dihydrolipoamide to lipoamide and NADH. Example (precursor) from human: DLDH_HUMAN, 509 amino acids (54.09 kDa). *See also* **oxoglutarate dehydrogenase complex**; **pyruvate dehydrogenase complex**.

dihydrolipoamide *S*-succinyltransferase EC 2.3.1.61; an enzyme that catalyses the formation of succinyl-CoA and dihydrolipoamide from *S*-succinyldihydrolipoamide and CoA. It is the E_2 component of the **oxoglutarate dehydrogenase complex**. Example from human (precursor): database code ODO2_HUMAN, 453 amino acids (48.69 kDa); the enzyme is formed from residues 68–453, 1–67 forming the transit peptide.

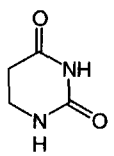
dihydrooratase EC 3.5.2.3; *systematic name*: (*S*)-dihydroorotate amidohydrolase; *other names*: carbamoylaspartic dehydrase; DHOase. An enzyme that catalyses the formation of *N*-carbamoyl-L-aspartate from (*S*)-dihydroorotate. In many eukaryotes this is an activity of **CAD protein**.

dihydropyridine receptor a protein located in skeletal muscle transverse tubules that specifically binds 1,4-dihydropyridine compounds. It forms one of the subunits of the L-type **calcium channel**.

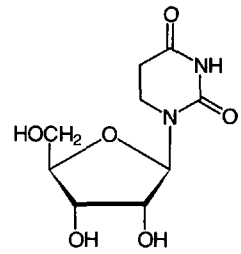
5α-dihydrotestosterone 4,5-dihydrotestosterone; 5α-androstan-17β-ol-3-one; a potent metabolite of testosterone, formed in the cytoplasm of target cells by the action of progesterone 5α-reductase, EC 1.3.1.30. It mediates many of the differentiating, growth-promoting, and functional actions of testosterone by binding to the **androgen receptor** and forming a complex. *See also* **testicular feminization**.



dihydrouracil 5,6-dihydrouracil, a minor pyrimidine base. It occurs in the **dihydrouridine arm** of **transfer RNA**.



dihydrouridine *symbol*: D *or* hU; 5,6-dihydrouracil riboside; 1-β-D-ribofuranosyl-5,6-dihydrouracil; a rare nucleoside occurring in the **dihydrouridine arm** of **transfer RNA**.



dihydrouridine

dihydrouridine arm *abbr.*: DHU arm; the base-paired segment of the **clover leaf structure** of **transfer RNA** that has attached to it the loop containing 5,6-dihydrouracil (see **dihydrouracil**).

dihydroxy+ *prefix (in chemical nomenclature)* indicating the presence of two substituent hydroxyl groups.

dihydroxyacetone *older name for* **glycerone**.

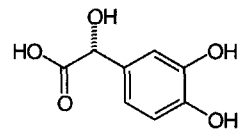
dihydroxyacetone phosphate *older name for* **glycerone phosphate**.

dihydroxyacetone synthase *see* **formaldehyde transketolase**.

dihydroxyacetone transferase *see* **transaldolase**.

dihydroxyeicosatetraenoate *abbr.*: diHETE; any of several products resulting from dioxygenation of arachidonate at two sites, normally resulting from **lipoxygenase** action on **hydroxyeicosatetraenoates**. (6*E*,8*Z*,10*E*,14*Z*)-(5*S*,12*S*)-5,12-dihydroxyeicosa-6,8,10,14-tetraen-1-oate (*abbr.*: 5(*S*),12(*S*)-diHETE) is synthesized in human leukocytes by two successive lipoxygenase reactions and acts as a leukotriene B_4 antagonist. *See* **leukotriene B**. (6*E*,8*Z*,11*Z*,13*E*)-(5*S*,15*S*)-5,15-dihydroxyeicosa-6,8,11,13-tetraen-1-oate (*abbr.*: 5(*S*),15(*S*)-diHETE) is synthesized in human neutrophils and enhances neutrophil degranulation. (5*Z*,9*E*,11*Z*,13*E*)-(8*S*,15*S*)-8,15-dihydroxyeicosa-5,9,11,13-tetraen-1-oate (*abbr.*: 8(*S*),15(*S*)-diHETE) is synthesized in human leukocytes, eosinophils, and platelets and is chemotactic for human polymorphonuclear leukocytes.

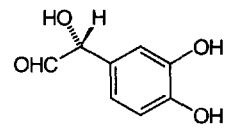
3,4-dihydroxymandelate an intermediate in the formation of 4-hydroxy-3-methoxymandelate from **norepinephrine**.



3,4-dihydroxyphenylalanine *see* **dopa**.

3,4-dihydroxyphenylethylamine *see* **dopamine**.

3,4-dihydroxyphenylglycolaldehyde the product of the action of monoamine oxidase on **norepinephrine**. It is converted by an NAD^+-dependent aldehyde dehydrogenase to 3,4-dihydroxymandelate.



1,25-dihydroxyvitamin D_3 *another name for* **calcitriol**.

diiodotyrosine *abbr.*: DIT; 3,5-diiodotyrosine; iodogorgoic acid, 3,5-diiodo-4-hydroxyphenylalanine, 2-amino-3-(3,5-diiodo-4-hydroxyphenyl)propanoic acid. Residues of the L enantiomer, together with residues of the monoiodo com-

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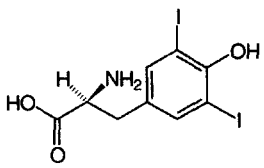
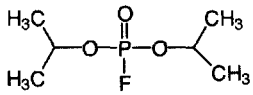
pound, 3-iodo-L-tyrosine, are formed by iodination of L-tyrosine residues in thyroglobulin as precursors of thyroid hormones.



diisopropylfluorophosphonate diisopropylfluorophosphate; dyflos; *abbr.*: DIPF *or* DFP; an inhibitor of **cholinesterase** and other **serine proteases**. It phosphorylates the serine in the enzyme's active site, causing long-lasting inhibition. Recovery of enzymic activity requires *de novo* enzyme synthesis.



diisopropylphospho *symbol*: Dip; *abbr.*: DIP; the doubly esterified phosphoric acyl group, $[(CH_3)_2CH–O–]_2P(O)–$, derived from diisopropyl fluorophosphate by loss of a fluorine atom.

dikaryon *or* **dicaryon** a living cell containing two nuclei, or a structure (e.g. a mycelium) composed of such cells. It may contain nuclei of the same genetic constitution (i.e. **homokaryons**) or of differing genetic constitutions (i.e. **heterokaryons**). —**dikaryotic** *or* **dicaryotic** *adj.*

diketose any monosaccharide derivative containing two (potential) ketonic carbonyl groups. *Compare* **ketose**.

dikinase either of the two enzymes belonging to the sub-subclass EC 2.7.9, comprising phosphotransferases with paired acceptors. For example, pyruvate,orthophosphate dikinase, EC 2.7.9.1, catalyses the reversible reaction:

ATP + pyruvate + orthophosphate = AMP + phospho*enol*pyruvate + pyrophosphate.

dil. *abbr. for* dilute (def. 2).

dilate to expand or cause to expand; to make larger or wider; e.g. of the pupil of the eye or a chamber of the heart. —**dilation** *or* **dilatation** *n.*

dilatometer any instrument for measuring small changes in the volume of liquids. One design consists of a (glass) bulb fitted with a graduated hollow stem in which changes in volume may be observed. In another design, the (glass) bulb is fitted with a stopper through which runs a capillary tube so that any increased volume of the contained liquid may escape; the change in mass of the bulb and its contained liquid may then be determined. —**dilatometry** *n.*

diluent a diluting agent; *see* **dilute** (def. 1).

dilute **1** **a** to lower the concentration of a solute in a solution (or of particles in a suspension). **b** to mix one fluid with another thereby lowering the concentration of the first. **2** *abbr.*: dil.; describing a solution (dispersion or mixture) having a relatively low concentration (of a specified solute, type of dispersed particle, or component). *Compare* **concentrated** (def. 1).

diluted (of a solution or suspension) lowered in concentration and increased in volume by addition of solvent or other diluent. *Compare* **concentrated** (def. 2).

dilution **1** the act or process of making more **dilute** (def. 2). **2** a diluted solution or suspension. **3** the (specified) extent to which a solution or suspension has been diluted.

dilution end-point analysis the determination of the concentration of antibody in a solution by allowing a given amount of antigen to react with increasing dilutions of the antibody. The most dilute solution that produces a detectable effect, e.g. precipitation, is taken as the end point.

dilution law *see* **Ostwald dilution law**.

dilution quenching the lowering of **counting efficiency** of a liquid scintillation counter by the addition of solvent to the contents of the scintillation vial. *See also* **quenching**.

dilution rate *symbol*: D; the rate, F, at which existing medium is replaced with fresh medium in a **continuous culture**, divided by the volume, V, of the culture: $D = F/V$. Under steady-state conditions the dilution rate numerically equals the specific growth rate of the culture. *See also* **auxostat**, **chemostat**.

dilution value of a buffer *symbol*: $(\Delta pH)_{½}$; the change in pH that occurs when a buffer solution is diluted with an equal volume of water.

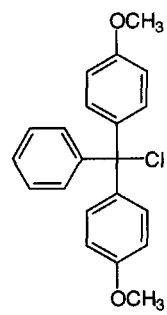
dimer **1** any molecular structure of any size in which two initially identical chemical entities have become covalently combined. **2** any macromolecular structure in which two (either identical or nonidentical) subunits are noncovalently associated. *See also* **heterodimer**, **homodimer**. —**dimeric** *adj.*

dimercaprol *or* **British anti-lewisite** (*abbr.*: BAL); 2,3-dimercaptopropanol; an antidote to the arsenical war gas, lewisite, that is also useful as a chelating agent and detoxicant for heavy-metal ions and as a protective agent for sulfhydryl groups in enzymes, coenzymes, or the like.

dimerize *or* **dimerise** cause a **dimer** to be formed. —**dimerization** *or* **dimerisation** *n.*

dimerizer hypothesis *or* **dimeriser hypothesis** an unsubstantiated model of facilitated diffusion proposed to explain the rates of entry of sugars into human erythrocytes from various mixtures of sugar species. According to this hypothesis, permeation occurs as a result of pairs of sugar molecules interacting with a membrane component, followed by the association of the sugars into dimers, a form in which a reduced number of free hydrogen-bond-forming groups would be available.

dimethoxytrityl *abbr.*: DMT; 4,4′-dimethoxytriphenylmethyl; a group used for protecting hydroxyl groups (especially the 5′-hydroxyl groups of nucleosides) during chemical synthesis or other procedures. It is usually introduced by reaction with dimethoxytrityl chloride, 4,4-dimethoxytriphenylmethyl chloride. *Compare* **trityl**.



4,4-dimethoxytriphenylmethyl chloride

dimethylallyl *trans*transferase EC 2.5.1.1; *systematic name*: dimethylallyl-diphosphate:isopentenyl-diphosphate dimethylallyl*trans*transferase; *other names*: prenyltransferase; geranyl-diphosphate synthase. An enzyme that catalyses the reaction of dimethylallyl diphosphate with isopentenyl diphosphate to form pyrophosphate and geranyl diphosphate. It participates in the pathway for the formation of **polyprenyl** groups, sesqui- and higher terpenes, and **cholesterol**.

dimethylaminoazobenzene isothiocyanate *see* **DABITC**.

dimethylaminoazobenzene sulfonyl chloride *see* **dabsyl**.

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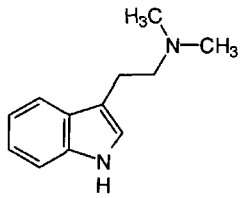
dimethylaminobenzaldehyde *see* **Ehrlich's reagent**.

dimethylaminonaphthalene sulfonyl chloride *see* **dansyl, dansylate**.

dimethylformamide *see* **DMF**.

dimethyltryptamine *N,N*-dimethyltryptamine; 3-[2-(dimethylamino)ethyl]indole; a hallucinogenic agent extracted from several plant species including *Piptadenia peregrina*. It is also a metabolite of 5-hydroxytryptamine. It is a controlled substance under the US Code of Federal Regulations.



dimorphism **1** the existence of a chemical compound in two distinct physical forms, e.g. two different crystalline forms. **2** the existence of individuals belonging to two distinct forms within the same species of organism; e.g. in **sexual dimorphism** the males and females of the same species are markedly different. **3** the occurrence in certain plants of two distinct forms of leaves or other parts in the same individual. —**dimorphic** *or* **dimorphous** *adj.*

dinactin *see* **nonactin**.

dinitrofluorobenzene *abbr.*: DNFB; *a (less correct) name for* fluorodinitrobenzene. *See* **Sanger's reagent**.

dinitrogen *systematic name for* the diatomic compound N_2, commonly termed (molecular) nitrogen.

dinitrophenate the strongly yellow-coloured anion, $(NO_2)_2$–C_6H_3–O^-, formed from dinitrophenol.

dinitrophenol *abbr.*: DNP; 2,4-dinitrophenol; a pale-yellow crystalline solid. It is a powerful uncoupler of **oxidative phosphorylation**, and hence toxic.

dinitrophenyl *symbol*: Dnp; the group formed by loss of the phenolic hydroxyl group from 2,4-dinitrophenol. *See* **Sanger's method**.

dinitrophenylate to introduce a dinitrophenyl group into a compound. —**dinitrophenylation** *n.*

dinoprost *a generic name for* prostaglandin $F_{2\alpha}$. *See* **prostaglandin**.

dinor+ *prefix (in chemical nomenclature)* indicating shortening of a carbon chain or contraction of a ring by two methylene groups. *See also* **nor+**.

Dintzis procedure a procedure for investigating the direction and rate of biosynthesis of a polypeptide. It requires the addition to a protein-synthesizing system *in vitro*, at a given time, of a **pulse** of a labelled form of an amino acid, of which there are several residues at different positions in the structure of the polypeptide. After various periods of elapsed time, within the time required for synthesis of a complete chain, completed molecules of the polypeptide are isolated, and the extents of incorporation of the labelled amino acid into them are determined for each position in which a residue occurs naturally. Over all the samples, a gradient of radioactivity (increasing from the N terminus to the C terminus of the chain) is found, indicating that the pulse tends to enter the more C-terminal positions and that the more N-terminal region has already been synthesized. By these means it was clearly shown for the first time that polypeptide chains are assembled from amino acids on a template and that synthesis takes place from its N terminus. [After Howard Marvin Dintzis (1927–), US biochemist, who conceived the procedure and described its use in 1961.]

dinucleotide **1** any **oligonucleotide** consisting of two mononucleotides in 3′–5′ phosphodiester linkage. **2** any **nucleotide coenzyme** in which either of the mononucleotides adenosine 5′-phosphate or adenosine 2′,5′-bisphosphate is in 5′–5′ diphosphate (i.e. phosphoric anhydride, pyrophosphate) linkage with nicotinamide mononucleotide or riboflavin 5′-phosphate.

dinucleotide fold *an alternative name for* **nucleotide binding fold**.

diode **1** a semiconductor device, containing one p–n junction, used in circuits to rectify **alternating current** to a **direct current**: semiconductor diode. **2** a thermionic valve containing an anode and a cathode and functioning in a similar manner: **thermionic diode**.

dioestrus *see* **estrous cycle**.

diol any organic compound (or portion of such a compound) containing two hydroxyl groups.

diol lipid any of various neutral lipids that are fatty-acid esters of dihydroxy alcohols (i.e. are not glycerides). They occur in small amounts in seed oils; e.g. 1-palmitoleoyl-2-*trans*-vaccenoyl-*erythro*-butane-2,3-diol, which is found in seeds of *Coix lachrima*.

dioxin receptor *see* **ARNT**.

dioxygen *systematic name for* the diatomic compound O_2, commonly termed (molecular) oxygen. *Compare* **trioxygen**.

dioxygenase any oxidoreductase enzyme of the sub-subclass EC 1.13.11. Such enzymes catalyse reactions involving the incorporation of both oxygen atoms of dioxygen into a second substrate; *see* e.g. **ethylene-forming enzyme**, **benzoate 1,2-dioxygenase**.

Dip *symbol for* the diisopropylphospho group.

DIP *abbr. for* the diisopropylphospho group.

dipentene a racemic mixture of the (+) and (–) enantiomers of **limonene**.

dipeptide any **oligopeptide** consisting of two (usually, α-) amino-acid residues.

dipeptide mimic any synthetic dipeptide that inhibits **angiotensin-converting enzyme**. An example is **captopril**.

dipeptidyl-peptidase *abbr.*: DPP; any member of a group of enzymes belonging to the sub-subclass EC 3.4.14, dipeptidylpeptide and tripeptidylpeptide hydrolases, that release an N-terminal dipeptide from an oligo- or polypeptide. **Dipeptidyl-peptidase I** (*or* cathepsin C), EC 3.4.14.1, is a lysosomal cysteine-type peptidase that acts on polypeptides, but not if the terminal amino-acid residue is Arg or Lys, and not if either of the adjacent residues is Pro. Example from *Rattus norvegicus*: database code CATC_RAT, 462 amino acids (52.38 kDa). **Dipeptidyl-peptidase II**, EC 3.4.14.2, is a lysosomal serine-type peptidase that acts preferentially on tripeptides. **Dipeptidyl-peptidase III**, EC 3.4.14.4 (*other names*: red cell angiotensinase; enkephalinase B), is a cytosolic serine-type peptidase that acts on tetra- or longer peptides. **Dipeptidyl-peptidase IV**, EC 3.4.14.5 (*other names*: dipeptidyl aminopeptidase IV; Xaa-Pro-dipeptidyl-aminopeptidase; Gly-Pro naphthylamidase; post-proline dipeptidyl aminopeptidase IV), catalyses the release of an N-terminal dipeptide, Xaa-Xbb-|-Xcc, from a polypeptide, preferentially when Xbb is Pro, provided Xcc is neither Pro nor hydroxyproline. The protein is a serine proteinase, type II transmembrane glycoprotein; it is a homodimer: database code DPP4_HUMAN, 766 amino acids (88.22 kDa); T-cell activation antigen CD26. **Dipeptidyl-dipeptidase**, EC 3.4.14.6, is a thiol-activated peptidase from *Brassica oleracea* that acts preferentially on tetrapeptides.

dip-F *symbol for* diisopropyl fluorophosphate.

DIPF *abbr. for* diisopropylphosphofluoridate. *See* **diisopropyl fluorophosphonate**.

diphenylamine reaction the reaction of an acidic solution of diphenylamine with deoxypentoses to give a blue colour. It is used in the quantitative determination of DNA, and alone or in combination with other reagents as a detection reagent.

2,5-diphenyloxazole *abbr.*: PPO; a compound used as a primary scintillant in scintillation counting. *See* **scintillation counter**. *See also* **scintillation cocktail**.

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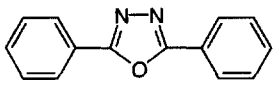


2,5-diphenyloxazole

diphosphate **1** the tetravalent anion, $P_2O_7^{4-}$, derived from diphosphoric acid (earlier known as pyrophosphoric acid), heptaoxodiphosphoric(V) acid, $(HO)_2PO–O–PO(OH)_2$. **2** any mixture of free diphosphoric acid and its anions. *see also* **inorganic diphosphate**, **pyrophosphate**. **3** any (partial or full) salt or ester of diphosphoric acid. **4** any organic compound containing two phosphoric residues linked by an oxygen atom. **5** name of the univalent group $–O–PO(OH)–O–PO(OH)_2$ (irrespective of its state of ionization). **6** *formerly*, any organic compound containing two independent phosphoric residues attached to different parts of the molecule; now incorrect, use **bisphosphate**.

(+)diphospho+ **1** *prefix to (or infix in)* a chemical name indicating the presence in ester (or diester) linkage of a diphosphoric residue. **2** *formerly*, *prefix* to a chemical name indicating the presence of two independent phosphoric residues in ester linkages; now incorrect, use **bisphospho+**.

diphosphoglycerate *former name for* **1 2,3-bisphospho-D-glycerate. 2 3-phospho-D-glyceroyl phosphate.**

diphosphoglycerate pocket *abbr.*: DPG pocket; *see* **bisphosphoglycerate pocket.**

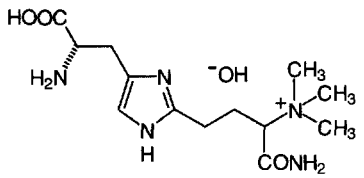
diphosphoinosotide *former name for* **phosphatidylinositol 4-phosphate.**

diphosphopyridine nucleotide (oxidized) *abbr.*: DPN; *obsolete name for* the oxidized form of nicotinamide adenine dinucleotide; *see* **NAD+**.

diphosphopyridine nucleotide (reduced) *abbr.*: DPNH; *obsolete name for* the reduced form of nicotinamide adenine dinucleotide; *see* **NADH**.

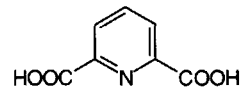
diphosphoric *symbol*: *PP or* (in the one-letter convention for nucleotides) pp; *general name for* a residue of diphosphoric acid, $(HO)_2PO–O–PO(OH)_2$, whether singly or multiply attached through oxygen to other groups and whether or not any residual hydroxyl groups are dissociated.

diphthamide a modified histidine residue on EF-2. *See* **elongation factor.**



diphtheria toxin an enzyme toxin produced by strains of *Corynebacterium diphtheriae* which are lysogenic for corynephage, whose genome contains the *tox* structural gene (carried by phage β*tox*$^+$). The toxin has the activity of EC 2.4.2.36; *recommended name*: NAD^+-diphthamide ADP-ribosyltransferase; *systematic name*: NAD^+:peptide-diphthamide *N*-(ADP-D-ribosyl)transferase. It catalyses the reaction between NAD^+ and peptide diphthamide to form nicotinamide and peptide *N*-(ADP-D-ribosyl)diphthamide. The toxin molecule is a proenzyme comprising a single polypeptide chain of ≈62 kDa; the toxin is lethal for susceptible animals at around 100 ng per kg of body mass. On cleavage of one peptide bond and one disulfide bond, the toxin splits into an N-terminal fragment, A (21.15 kDa), the enzyme that specifically inhibits protein synthesis by catalysing transfer of the ADP-ribosyl moiety of NAD^+ to eukaryotic EF-2 (*see* **elongation factor**) in the cytoplasm, and a C-terminal fragment, B (≈40 kDa), that is required for recognition of specific surface receptors on sensitive cell membranes. Fragment B is necessary for the toxicity of fragment A because it enables the latter to cross the plasma membrane. Example (precursor) from phage β: database code DTX_CORBE, 567 amino acids (61.53 kDa); fragment A, amino acids 33–225; fragment B, amino acids 226–567.

dipicolinate 2,6-pyridinedicarboxylate; a substance that is abundant (10%) in bacterial spores. Its production is a striking feature of sporulation and it may play a part in making spores resistant to heat.



dipicolinic acid

diplochromosome a 'double chromosome', comprising the arms of two daughter chromosomes attached to a single centromere. It arises due to failure of the centromere to divide following duplication of a chromosome.

diploid describing a cell or nucleus having two sets of homologous **chromosomes**; i.e. containing twice the **haploid** number. —**diploidy** *n.*

diploid state the chromosome state of a cell in which each type of chromosome, except for the sex chromosomes, is always represented twice.

diplotene the fourth phase of prophase I in **meiosis**.

dipolar bond *or* **coordinate bond** *or* **coordinate covalence** *or* **coordinate link** *or* **dative bond** *or* **semipolar double bond** a covalent bond formed (actually or conceptually) between two initially uncharged moieties by **coordination** (def. 2). The consequent generation of opposing charges on the linked structures creates a **dipole**; e.g.

$$R_3N: + \ddot{O}: \rightarrow R_3N^+–\ddot{O}:^-.$$

The term is preferred to the alternatives, which are now either obsolescent or obsolete. *Compare* **polar bond**.

dipolar correlation time time taken for an atomic spin system to rotate through one radian from its previous orientation, the rotation being caused by interactions with other, neighbouring spins.

dipolar interaction the interaction between two **magnetic moments** due to the effect of the magnetic field of one on the other.

dipolar ion *or* **zwitterion** a molecule containing ionic groups of opposite charge in equal numbers. *Compare* **amphion**.

dipole a pair of equal and opposite electric charges or magnetic poles (especially in a molecular entity) separated by a, usually, small distance. —**dipolar** *adj.*

dipole moment *or* **electric dipole moment** *symbol*: $\boldsymbol{p}$ *or* μ; a vector quantity equal to the product of the absolute magnitude of either charge in a dipole (the two are equal in an uncharged molecule) multiplied by the distance separating them. If a molecule possessing a dipole moment is placed in a uniform electric field, it will be subject to torque tending to line it up in the direction of the field. $\boldsymbol{p} = \Sigma Q_i \boldsymbol{r}_i$ coulomb metres, where Q_i is the charge and $\boldsymbol{r}_i$ is the position vector.

dipyridamole an inhibitor of cyclic AMP phosphodiesterase and 5-lipoxygenase, used as a coronary vasodilator.

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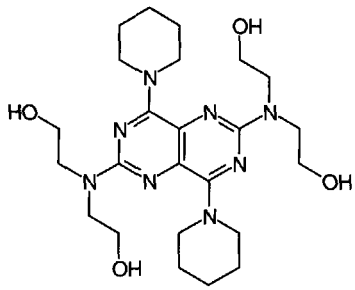


dipyridamole

diradical *an alternative term for* **biradical**.

direct current *abbr.*: d.c. *or* DC; an electric current that flows in only one direction.

directional selection any genetic **selection** that shifts the population mean in the direction desired by the breeder.

dis+ *prefix* indicating **1** reversal. **2** deprivation, exclusion, or lack. **3** negation. **4** removal or release.

dis2 a gene in fission yeast that is the equivalent of ***DIS2 S1*** in budding yeast.

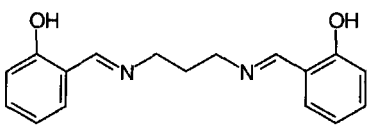
disabled strain any strain of organism, especially a microorganism, that because of some character, e.g. a nutritional requirement, is unable to reproduce in the normal environment, including the normal host, and can only survive in laboratory conditions.

disaccharidase any enzyme within sub-subclass EC 3.2.1 that hydrolyses a disaccharide to its constituent monosaccharides.

disaccharidase deficiency *see* **lactase deficiency**.

disaccharide any **oligosaccharide** consisting of two monosaccharide residues. It may be a **nonreducing disaccharide** or a **reducing disaccharide**, depending on the mode of linkage between the residues.

disalicylidenepropanediamine *abbr.*: DSPD; *N,N'*-disalicylidene-1,3-diaminopropane; an inhibitor of photosynthetic electron flow at the ferredoxin level.



disassociation *a variant form of* **dissociation** (def. 1).

disc *a variant spelling (esp. Brit.) of* **disk**.

discharge **1** *(in physics)* the release of an electric charge, e.g. from a condenser or a battery, or the equalization of an electric potential difference. **2** *(in physics)* the intermittent or continuous flow of electricity through a gas by the formation of electrons and ions. **2** *(in medicine)* an abnormal secretion from a body cavity, or the secretion from a wound.

discoidin any of a group of endogenous carbohydrate-binding proteins (lectins) produced by cells of the slime mould *Dictyostelium discoideum* during differentiation. Similar to **pallidin**, they may be concerned in cell adhesion. Examples (all from *D. discoideum*): discoidin I, A chain: database code DISA_DICDI, 253 amino acids (28.24 kDa); B and C chains: database code DISC_DICDI, 253 amino acids (28.39 kDa).

discontinuous epitope an immunological determinant (i.e. **epitope**) on an antigen that comprises different sections of a protein molecule brought together by folding of the polypeptide chain. *Compare* **continuous epitope**.

discriminator **1** any (electronic) device that gives an output signal only when the input signal is above a certain preset level or has certain preset characteristics. **2** any criterion used in sorting objects, experimental results, signals, etc.

disease any anatomical abnormality or impairment of the normal functioning of an organism or of any of its parts other than one arising directly from physical injury. It may be caused by environmental factors (e.g. malnutrition, toxic agents, etc.), infective agents (bacteria, viruses, etc.), inherent defects in the organism (e.g. genetic disease), or any combination of these factors.

disequilibrium assay any radioimmunoassay in which the reagents are not added at the same time and are not allowed to reach thermodynamic equilibrium. *Compare* **equilibrium assay**.

disinfection the destruction or removal of all organisms capable of giving rise to infection. *Compare* **sterilize** (def. 1).

disintegration *or* **nuclear disintegration** any process of nuclear **decay** involving a splitting into more nuclei or the emission of particles (either spontaneously or as a result of a collision).

disintegration constant *or* **decay constant** *symbol*: λ; for a radionuclide, the probability of the nuclear decay of one of its nuclei in unit time. It is given by:

$$\lambda = -(1/t)\ln(A/A_0),$$

where A_0 is the radioactivity at zero time and A is the activity at time t. *See also* **average life**.

disintegrin any of a group of compounds that act as inhibitors of platelet–fibrinogen interaction and other aggregations. They are found in certain snake venoms. Example, disintegrin CTF-I/CTF-II from *Trimeresurus flavoviridis*: database code DISC_TRIFL, 75 amino acids (8.32 kDa); two motifs. Example, from *Agkistrodon rhodostoma* (Malayan pit viper) venom: database code DISI_AGKRH, 68 amino acids (7.32 kDa).

disjunction the separation of chromosomes at **anaphase** during nuclear division.

disk *or (esp. Brit.)* **disc** **1** a circular, flattened structure, or any object having or resembling such a shape. *See also* **retinal rod**. **2.** *(in computing)* a disk-shaped device on which files are stored electromagnetically.

disk (gel) electrophoresis a technique of separation by electrophoresis in which a tube is loaded first with the sample, applied in a gel support (usually polyacrylamide), followed by a spacer gel and finally by the running gel, in which separation occurs. The gels are so formed as to give a gradient of progressively smaller pore size, and a discontinuous buffer system is used. This arrangement causes the separating components of the applied mixture to stack as a series of very thin bands and permits very high resolution.

dismembrator an ultrasonic device for rapidly disrupting cells in bacteriological and cytological studies. It consists of a probe oscillating at ≈20 kHz and an acoustical power of up to 150 W that is dipped into a cell suspension, contained in either a stainless-steel or glass beaker.

dismutase *see* **superoxide dismutase**.

dismutation a chemical reaction in which a single compound serves both as an oxidizing agent and as a reducing agent; e.g. the reaction of two molecules of pyruvate and one of water giving rise to one molecule each of lactate, acetate, and carbon dioxide. *Compare* **disproportionation**.

disodium chromoglycate *see* **cromolyn**.

disodium etidronate *see* **etidronate**.

disome a **polysome** in which two ribosomes are attached to a strand of messenger RNA. *Compare* **monosome**, **nucleodisome**.

Dispase *proprietary name for* a highly stable neutral metalloproteinase obtained from *Bacillus polymyxa*. It is so named from its use, alone or with collagenase, for gentle enzymic disaggregation and dispersal of animal tissues into separated cells for primary **cell culture** and for redispersal of cells on subculturing. *See also* **Chaotropase**, **Pronase**.

disperse phase *or* **dispersed phase** the phase in a two-phase sys-

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tem that consists of the particles in a colloid, emulsion, or suspension.

dispersion **1** the selective separation of an inhomogeneous emission according to some criterion (especially frequency, particle mass, speed, or energy); e.g. the separation of heterochromatic light into its components. **2** any system in which particles of any nature (e.g. solid, liquid, gas, or composite) are dispersed in a solid, liquid, or gas of different composition. **3** *(in statistics)* the extent to which values of a statistical frequency distribution are scattered around a mean or median value.

dispersion force *or* **London force** a long-range attractive interaction occurring between atoms or molecules whether or not they have permanent charges or dipole moments. Since the electrons in an atom or molecule are moving, an instantaneous dipole moment is induced in the atom or molecule; this averages to zero over a short time. This instantaneous dipole moment will induce an oppositely oriented dipole moment in a neighbouring atom or molecule in a manner that does not time-average to zero. This interaction energy, $V(R)$, is given approximately by:

$$V(R) = -\frac{3}{2}\left(\frac{h\nu_A\nu_B}{\nu_A+\nu_B}\right)\frac{\alpha_A\alpha_B}{(4\pi\varepsilon_0)}\frac{1}{R^6}$$

where ν_A and ν_B are the approximate frequencies of the first electron transitions of entities A and B, α_A and α_B are their polarizabilities, ε_0 is the permittivity of vacuum, h is the Planck constant, and R the distance between the entities. [After Fritz London (1900–54), German-born US physicist.]

dispersive replication of DNA *see* **replication of DNA**.

displacement binding a technique in which the displacement of radioligand bound to a population of receptors is measured as the concentration of an unlabelled ligand, which binds to the same receptors, is increased. It is used to distinguish different affinity states of the receptor population or receptor selectivity of the radioligand.

displacement chromatography an analytical chromatographic technique in which a mixture is applied to a chromatographic column and the components of the mixture are then successively displaced by elution with a solution containing another substance of higher affinity for the column material than that of the most firmly held component. The relative proportions of the components of the mixture are determined by **frontal analysis** of the eluate.

displacement electrophoresis *an alternative term for* **isotachophoresis**.

displacement loop *an alternative name for* **D-loop**.

displacement reaction a chemical reaction in which an atom or group is displaced from its covalent attachment to a central (frequently a carbon) atom following an attack by either an **electrophile** or a **nucleophile**.

disproportionation any chemical reaction of the type:

$$A + A \rightarrow A' + A'',$$

where A, A′, and A″ are different chemical species. *Compare* **dismutation**.

DIS2 S1 a gene of budding yeast encoding protein phosphatase I (its equivalent in fission yeast is ***dis2***). In the absence of gene function **mitosis** is arrested. The product in *Saccharomyces cerevisiae* is: database code YSCDIS2S1A, 312 amino acids (35.93 kDa).

dissimilation *a less common alternative term for* **catabolism**. *Compare* **assimilation**. —**dissimilatory** *adj.*

dissimilatory nitrate reduction *see* **nitrate reduction**.

dissociation **1** *or* **disassociation** a reversible splitting of a chemical substance into simpler entities; *compare* **association**. In this sense, the term may be applied to: **a** the **heterolysis** of a covalent bond, yielding, in the case of an initially uncharged molecule, positively and negatively charged ions: **ionic dissociation**; **b** the disaggregation of a macromolecular homopolymer or heteropolymer into its constituent units (i.e. **protomers**), usually by a stepwise process through components of intermediate size (i.e. **oligomers**) and without rupture of covalent bonds; **c** the breakdown of an enzyme–substrate complex, which may or may not involve cleavage of a covalent bond; or **d** the separation of a complex of two or more molecules into the constituent molecules. **2** a splitting of a chemical substance by the **homolysis** of a covalent bond, yielding **radicals**. **3** **translocation** between a large chromosome and a small supernumerary one, in effect splitting the large chromosome into two chromosomes. **4** separation (induced or spontaneous) of the nuclear components of a heterokaryotic **dikaryon**. —**dissociated**, **dissociable**, **dissociative** *adj.*; **dissociate** *vb.*

dissociation constant *symbol*: K_{diss} *or* K_d; the **equilibrium constant** for the reversible breakdown of a complex or a chemical compound into two or more simpler entities; the reciprocal of the **association constant**, K_{ass}. In some cases, an **apparent dissociation constant** (K'_d) is determined (for the distinction *see* **equilibrium constant**). It is also known as the **ionization constant** in cases where a substance dissociates into ions. For a dissociation (or ionization) of the general type $AB \rightleftharpoons A + B$, the dissociation (or ionization) constant is given by:

$$K_{diss} = [A][B]/[AB] = 1/K_{ass}.$$

dissociation energy *symbol*: D; the enthalpy (per mole) required to break a given chemical bond in a specified chemical entity by homolysis.

distal situated furthest from an origin, central line, or point of attachment.

distal protein a protein that binds late in the assembly of complex structures, such as ribosomes. *Compare* **proximal protein**.

distil *or (US)* **distill** to undergo, to subject to, to purify, or to separate by **distillation**.

distillate the liquid (or solid) product of **distillation**.

distillation the act or process of evaporating a liquid by boiling so that its components, which are vaporized at different temperatures or at different rates, can be separated and condensed back to a liquid (or solid). It is used to purify one liquid from a mixture of liquids or from (dissolved) solids. *See* **fractional distillation**.

distribution **1** *(in chemistry) an alternative term for* **partition**. **2** *(in biochemistry)* the pattern of occurrence of a substance within or between cells or tissues, or within a group of organisms, taxa, etc. **3** *(in biology)* the geographical range or pattern of occurrence of a particular taxon or genetic variant. **4** *(in statistics)* the frequency of occurrence of a variable at each of a number of discrete values. *See also* **normal distribution**.

distribution coefficient **1** *an alternative term for* **partition coefficient**. **2** in **gel chromatography**, the fraction of the stationary phase that is available for diffusion of a given solute species.

distribution law *an alternative name for* **partition law**.

distributive **1** of, relating to, or characterized by distribution. **2** *(in molecular biology) or* **nonprocessive** describing (the action of) any enzyme or catalytic complex that progressively synthesizes or degrades a biopolymer by effecting several or many cycles of the same type of reaction or reaction sequence and dissociates from the template or intermediate product after each catalytic event. *Compare* **processive**. —**distributively** *adv.*

disulfide *or* **disulphide** *(in organic chemistry)* any compound containing two bivalent sulfur atoms linked by a covalent bond and each attached to a carbon atom.

disulfide bond *or* **disulfide bridge** *or* **disulfide link** a covalent bond between two sulfur atoms. Such bonds in biomolecules are usually formed by the oxidation of **sulfhydryl groups** in two neighbouring cysteine molecules or residues. Disulfide bonds may link two half-cystine residues in the same polypeptide chain, as in ribonuclease, or in different peptide chains, as in insulin or oxidized glutathione, and they often are important in maintaining the three-dimensional structure of polypeptides and proteins. They may also be reversibly formed in oxidation–reduction reactions as in the interconversion of

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lipoamide and dihydrolipoamide. Also: **disulphide bond** *or* **disulphide bridge** *or* **disulphide link**.

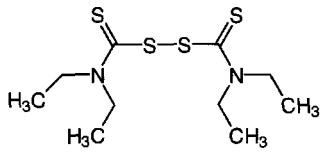
disulfide interchange *or* **disulphide interchange** any chemical reaction in which there is an interchange in the groups attached to two or more disulfide bonds; e.g.:

$$R\text{–}S\text{–}S\text{–}X + Y\text{–}S\text{–}S\text{–}Z \rightleftharpoons R\text{–}S\text{–}S\text{–}Y + X\text{–}S\text{–}S\text{–}Z,$$

where R, X, Y, and Z are different polypeptide chains or other SH-bearing molecules. *See also* **protein disulfide isomerase**.

disulfide knot *or* **disulphide knot** a region at the centre of a **fibrinogen** molecule where the six polypeptide chains are linked together by eight disulfide bonds. *Compare* **cystine-knot**.

disulfiram *trivial name for* tetraethylthiuram disulfide; bis(diethylthiocarbamoyl) disulfide; a drug used to deter alcohol abuse in the treatment of alcoholism. Alcohol ingestion after disulfiram causes vasomotor disturbances, nausea, vomiting, and even unconsciousness and death. It acts by inhibiting the enzyme acetaldehyde dehydrogenase and hence slows the removal of acetaldehyde. It occurs naturally in the otherwise edible fruit body of the agaric mushroom *Coprinus atramentarius*. One proprietary name is Antabuse.



DIT *abbr. for* diiodotyrosine.

dithioerythritol *abbr.*: DTE; *erythro*-1,4-dimercapto-2,3-butanediol; both this and **dithiothreitol** are known as **Cleland's reagent**. It has similar properties to dithiothreitol but is less often used.

dithiothreitol *abbr.*: DTT; *threo*-1,4-dimercapto-2,3-butanediol; both this and **dithioerythritol** are known as **Cleland's reagent**. A water-soluble solid compound which, because of its low redox potential (–0.33 V, pH 7.0), is capable of maintaining monothiols completely in the reduced state and of reducing disulfides quantitatively, so becoming oxidized to a cyclic disulfide; it has little tendency to be oxidized directly by air.

diuresis increased or excessive flow of urine.

diuretic **1** producing an increase in the volume of urine. **2** any agent that increases the volume of urine.

diurnal **1** occurring during the day. **2** repeating every day; having a periodicity of approximately 24 hours. *Compare* **circadian**.

Diuron *see* **DCMU**.

divergent evolution *or* **divergence** biological evolution that tends to produce an increasing difference in some characteristic(s) between initially similar groups of, e.g., organisms or gene products. *Compare* **convergent evolution**.

divergent transcription the transcription of adjacent genes from opposite strands of duplex DNA and in opposite directions.

dixenic *see* **synxenic**.

Dixon plot a graphical method for the presentation of enzyme-kinetic data by which a Michaelis constant, K_m (*see* **Michaelis kinetics**), or an **inhibitor constant**, K_i, may be determined. The method is primarily used as a means of readily obtaining K_i. The reciprocal of the initial velocity (i.e.$1/V$) is plotted against a series of inhibitor concentrations [I], at constant substrate concentration, [S]. When this is done for a number of values of [S], the resulting lines intersect at a point corresponding to K_i. The value of [I] at which this occurs is to the left of the ordinate (for competitive inhibition) and corresponds to $-K_i$. For non-competitive inhibition the lines meet on the abscissa. [After Malcolm Dixon (1899–1985), British enzymologist, who described it in 1972.]

dizygotic describing twin offspring formed from two separate ova fertilized by two separate sperms. *Compare* **monozygotic**.

DL *prefix (in chemical nomenclature)* denoting an equimolar mixture of D and L enantiomers. *See* **D/L convention**.

dl- *prefix (in chemical nomenclature)* formerly used to denote **racemic**; now obsolete, use (±)-, *racemo*-, or *rac*-.

D/L convention a convention of symbols used to designate the **absolute configuration** around a chiral element in α-amino acids, cyclitols, monosaccharides, and derivatives of these classes of compounds. Within these classes it can be applied to any molecule of the type R_1CHXR_2 that can be oriented in a **Fischer projection** with the most highly oxidized atom at the top; then if X is on the right the configuration is designated by the prefix D-, whereas if X is on the left the configuration is designated by the prefix L-, relative to D-(+)- or L-(–)-glyceraldehyde. Racemic (i.e. equimolar) mixtures of D and L enantiomers are designated by the prefix DL-. α-Amino acids are designated D- or L- according to the configuration at the α-carbon atom. Cyclitols are designated D- when the formula is drawn in such a way that the substituent on the lowest-numbered asymmetric carbon atom is above the plane of the ring and the numbering is anticlockwise, and L- when it is clockwise; the locant of the defining centre should precede the prefix D- or L-, e.g. 1D-1-*O*-methyl-*myo*-inositol. For monosaccharides the highest-numbered chiral centre (i.e. carbon atom) is the reference atom determining whether the monosaccharide is D or L. When a compound contains more than one class of residue the configuration designators are D_s or L_s if they apply to an amino-acid residue, D_c or L_c to a cyclitol residue, and D_g or L_g to a monosaccharide residue (the subscript s denoting the reference α-amino acid serine, the subscript c denoting cyclitol, and the subscript g denoting the reference monosaccharide glyceraldehyde). The absolute configurations of chiral compounds of classes other than those listed are designated by application of the **sequence rule**. *Compare* ***ambo-***, ***d-***, ***l-***, ***dl-***, **isomerism**.

D-loop *or* **displacement loop** a DNA structure generated when an additional strand of DNA is taken up by a DNA duplex, so that one strand of the original duplex is displaced, forming a D-shaped loop. Formation of a D-loop is favoured in negatively supercoiled DNA and can occur spontaneously. Such D-loops are formed in covalently closed mammalian mitochondrial DNA, and are prominent as intermediates in genetic recombination, in which their formation is catalysed by strand-exchange enzymes, the best characterized of which is the RecA protein of *Escherichia coli*.

DMF *or* **DMFA** *abbr. for* *N*,*N*-dimethylformamide; a neutral liquid of low melting point (–61 °C) and a reasonably high boiling point (153 °C), miscible with water and with most common organic solvents, hence sometimes termed the **universal solvent**.

DMSO *abbr. for* dimethylsulfoxide (use discouraged, Me_2SO preferred).

DMT *abbr. for* the dimethoxytrityl group.

dna symbol for any of various bacterial genes that are involved in DNA replication. For example, *dnaG* is the gene for **DNA primase** in *Escherichia coli*.

DNA *abbr. and common name for* **deoxyribonucleate** (def. 1), or **deoxyribonucleic acid**; one of the two main types of **nucleic acid**, consisting of a long, unbranched macromolecule formed from one, or more commonly, two, strands of linked deoxyribonucleotides, the 3′-phosphate group of each constituent deoxyribonucleotide being joined in 3′,5′-phosphodiester linkage to the 5′-hydroxyl group of the deoxyribose moiety of the next one. *Compare* **RNA**. The absence of a 2′-hydroxyl group on each deoxyribose moiety renders these phosphodiester linkages resistant to hydrolytic attack by alkali, in contrast to those of RNA. A DNA strand, unless circular, has polarity, with one **5′ end** and one **3′ end**, the two strands in duplex DNA having opposed polarities. Two purines, adenine and guanine, and two pyrimidines, cytosine and thymine, are the major bases present. The linear sequence of the purine and pyrimi-

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dine bases carries genetic information, whereas the deoxysugar and phosphoric residues play a structural role; the base sequence is written in the 5′→3′ direction. *See also* **double helix**. Specific forms, functions, molecules, or preparations of DNA may be designated by prefixes or suffixes, thus:

A-DNA *or* **DNA-A**, **A form** of DNA; **amDNA**, **anti-messenger DNA**; **B-DNA** *or* **DNA-B**, **B form** of DNA; **cDNA**, **complementary DNA**; **cccDNA**, **covalently closed circular DNA**; **C-DNA** *or* **DNA-C**, **C form** of DNA; **ctDNA**, chloroplast DNA; **dsDNA**, double-strand(ed) DNA (*see* **duplex DNA**); **iDNA**, **intercalary DNA**; **msDNA**, **multicopy single-strand(ed) DNA**; **mtDNA**, **mitochondrial DNA**; **nDNA**, nuclear DNA; **pDNA**, plasmid DNA; **rDNA**, **ribosomal DNA**; **recDNA**, **recombinant DNA**; **rfDNA**, **replicative-form DNA**; **rtDNA**, **recombinant DNA**; **scDNA**, **single-copy DNA**; **ssDNA**, **single-strand(ed) DNA**; **tDNA**, **transfer DNA**; **T-DNA**, transfer DNA of the **Ti plasmid**. *See* full entry for **T-DNA**. **Z-DNA** *or* **DNA-Z**, **Z form** of DNA.

DNAase *or* **DNAse** *abbr.* sometimes used for **deoxyribonuclease**; DNase is more usual.

DNA-binding protein F/G *see* **matrin**.

DNA blot transfer *see* **blot-transfer technique**.

DNA chip *see* **SBH**.

DNA cloning *see* **molecular cloning**.

DNA cycle *see* **cell-division cycle**.

DNA-dependent DNA polymerase *see* **DNA polymerase**.

DNA-dependent RNA polymerase *see* **RNA polymerase**.

DNA-directed DNA polymerase *recommended name for* **DNA polymerase**, EC 2.7.7.7.

DNA-directed RNA polymerase *recommended name for* **RNA polymerase**, EC 2.7.7.6.

DNA fingerprinting a term sometimes used to refer to **genetic profiling**.

(DNA) glycosylase *or* **DNA glycosidase** any of a group of glycohydrolases that initiate repair of DNA by hydrolysing N-glycosyl bonds linking deoxyribose residues with modified or incorrect bases to generate apurinic or apyrimidinic sites in the DNA and release the bases. They include DNA-3-methyladenine glycosidase I (EC 3.2.2.20), DNA-3-methyladenine glycosidase II (EC 3.2.2.21), and formamidopyrimidine-DNA glycosidase (EC 3.2.2.23). The enzymes form part of the pathway of base-excision repair, which acts on oxidative or non-oxidative damage, as determined by the specificity of individual enzymes. Sequences tend to be related; examples from *Escherichia coli*: DNA-3-methyladenine glycosidase I is constitutive and specific to the named base: database code 3MG1_ECOLI, 187 amino acids (21.08 kDa); DNA-3-methyladenine glycosidase II is inducible and releases any of 3-methyladenine, 3-methylguanine, 7-methylguanine, *O*-2-methylthymine, and *O*-2-methylcytosine: database code 3MG2_ECOLI, 282 amino acids (31.36 kDa).

DNA gyrase *see* type II **DNA topoisomerase**.

DNA helicase an enzyme that catalyses unwinding of the DNA double helix during DNA replication and repair. It requires ATP. Example, *rep* gene product from *Escherichia coli*: database code REP_ECOLI, 673 amino acids (76.85 kDa).

(DNA) joinase *an alternative name for* **DNA ligase**.

DnaK *or* **heat-shock protein 70** *abbr.*: hsp70; a **heat-shock protein** that plays an essential role in the initiation of DNA replication in **lambda phage** and, in combination with DnaJ protein, acts to release proteins O and P. Example from *Escherichia coli*: database code DNAK_ECOLI, 637 amino acids (68.98 kDa).

DNA ligase *or* **(DNA) joinase** *or* **DNA repair enzyme** either of two enzymes that restore broken phosphodiester bonds in deoxyribonucleic acids. (1) **DNA ligase (ATP)** EC 6.5.1.1; *systematic name*: poly(deoxyribonucleotide):poly(deoxyribonucleotide) ligase (AMP-forming); *other names*: polynucleotide ligase; DNA repair enzyme; (DNA) joinase; *former name*: sealase. An enzyme that catalyses the reaction:

$$\text{ATP} + (\text{deoxyribonucleotide})_n + (\text{deoxyribonucleotide})_m = \text{AMP} + \text{pyrophosphate} + (\text{deoxyribonucleotide})_{n+m}.$$

Example from phage T4: database code DNLI_BPT4, 487 amino acids (55.23 kDa). (2) **DNA ligase (NAD$^+$)** EC 6.5.1.2; *systematic name*: poly(deoxyribonucleotide):poly(deoxyribonucleotide) ligase (AMP-forming, NMN-forming); *other names*: polynucleotide ligase (NAD$^+$); DNA repair enzyme; (DNA) joinase. An enzyme that catalyses the reaction:

$$\text{NAD}^+ + (\text{deoxyribonucleotide})_n + (\text{deoxyribonucleotide})_m = \text{AMP} + \text{nicotinamide mononucleotide} + (\text{deoxyribonucleotide})_{n+m}.$$

Example from *Escherichia coli*: database code DNLJ_ECOLI, 671 amino acids (73.61 kDa).

DNA-like RNA *abbr.*: D-RNA *or* dRNA; a minor fraction of eukaryotic cellular RNA that has a base composition much closer to that of DNA than the bulk of RNA. It is mainly of high molecular mass, short half-life, and confined to the nucleus, and is probably the same as **giant messenger-like RNA** and **pre-messenger RNA**.

DNA-3-methyladenine glycosidase *see* **(DNA) glycosylase**.

DNA methylase either of two enzymes involved in **modification** and other roles. (1) **Site-specific DNA-methyltransferase (adenine-specific)** EC 2.1.1.72; *other names*: *N*-6 adenine-specific DNA methylase; modification methylase; restriction–modification system; it catalyses the reaction:

S-adenosyl-L-methionine + DNA-adenine = *S*-adenosyl-L-homocysteine + DNA-6-methylaminopurine.

Example from *Escherichia coli*: database code DMA_ECOLI, 278 amino acids (32.06 kDa); it recognizes the base sequence GATC and is part of the system for postreplicative mismatch repair. (2) **Site-specific DNA-methyltransferase (cytosine-specific)** EC 2.1.1.73; *other names*: *C*-5 cytosine-specific DNA methylase; modification methylase; restriction–modification system; it catalyses the reaction between *S*-adenosyl-L-methionine and DNA-cytosine to form *S*-adenosyl-L-homocysteine and DNA-5-methylcytosine. Example from *E. coli*: database code DCM_ECOLI, 472 amino acids (53.40 kDa); it recognizes the base sequence CCWGG and methylates both strands.

(DNA) nicking–closing enzyme *or* **nicking-and-closing enzyme** *alternative names for* type I **DNA topoisomerase**.

DNA nucleotidylexotransferase *recommended name for* **terminal deoxynucleotidyltransferase**.

DNA photolyase EC 4.1.99.3; *recommended name*: deoxyribodipyrimidine photo-lyase; *other name*: photoreactivating enzyme. An enzyme that splits cyclobutadipyrimidine (in DNA) into two pyrimidine residues (in DNA), thereby repairing the DNA after light-induced **pyrimidine dimer** formation. It is light dependent, requiring the cofactors reduced flavin and either (in different enzyme types) a folate coenzyme or a modified flavin. Example, *Escherichia coli* enzyme required for 'light repair': database code PHR_ECOLI, 472 amino acids (53.61 kDa); four motifs.

DNA polymerase *common name for* either of two categories of enzymes that catalyse the synthesis of DNA from deoxyribonucleoside triphosphates in the presence of a nucleic-acid primer. Based on structural similarities, DNA polymerases have been grouped in two families. In family A are *Escherichia coli* and various other bacterial polymerases I, *Thermus aquaticus* Taq polymerase, some bacteriophage polymerases, and yeast mitochondrial polymerase γ. In family B are many polymerases of higher eukaryotes, yeast polymerases I to III, and polymerase REV3, *E. coli* polymerase II, archaebacterial polymerases, and many viral polymerases.

(1) **DNA-directed DNA polymerase** EC 2.7.7.7; *other name*: DNA nucleotidyltransferase (DNA-directed); it is required for DNA replication and repair and has 3′-exonuclease activity (*see* **proofreading**). Eukaryotic DNA-directed DNA polymerases are of five types:

(a) DNA polymerase-α (also called DNA polymerase I *or* Kornberg enzyme) is a high-molecular-mass (>100 kDa) en-

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zyme that was first detected in *E. coli*; in association with **DNA primase** it is replicative. Example (human): database code DPOA_HUMAN, 1462 amino acids (165.67 kDa) belongs to polymerase family B, with six conserved regions, four of which are involved in substrate binding. Several DNA viruses have type B polymerases; examples include adenoviruses and herpesviruses.

(b) DNA polymerase-β (*or* DNA polymerase II) is a low-molecular-mass (<50 kDa) enzyme recovered almost entirely in nuclear extracts.

(c) DNA polymerase-γ (*or* DNA polymerase III) is an enzyme of high molecular mass (>100 kDa) that copies synthetic polyribonucleotides with high efficiency, but does not copy DNA well. Examples from *E. coli*: α chain: database code DP3A_ECOLI, 1160 amino acids (129.76 kDa); β chain: database code DP3B_ECOLI, 366 amino acids (40.54 kDa); ε chain: database code DP3E_ECOLI, 243 amino acids (27.07 kDa). The protein at database code DP3X_ECOLI, 643 amino acids (71.06 kDa) represents ε and τ; the production of the two protein products from this region is due to programmed ribosomal frameshifting.

(d) DNA polymerase-δ is a zinc finger protein with both polymerase and 3′-exonuclease activities; it is a heterodimer of 125 kDa and 50 kDa subunits.

(e) DNA polymerase-mt is the mitochondrial DNA polymerase.

E. coli has three DNA polymerases: (a) pol I, database code DPO1_ECOLI, 928 amino acids (103.00 kDa); this has 5′- and 3′-exonuclease activities; the 5′-exonuclease activity is involved in DNA replication; the polymerase activity is employed during DNA repair; 3-D structures are known for parts of the enzyme (database codes NRL_1DPI1 and NRL_1DPI2). (b) pol II, database code DPO2_ECOLI, 782 amino acids (89.82 kDa); is regulated by **lexA** and belongs to family B (above). (c) pol III, the major replication polymerase, has an α subunit with polymerase activity, database code DP3A_ECOLI, 1160 amino acids (129.76 kDa) and a total subunit composition of $(\alpha,\varepsilon,\theta)_2$-$\tau_2$-$(\gamma,\delta,\delta',\psi,\chi)_2$-$\beta_4$. The complex $(\alpha,\varepsilon,\theta)$, the 'core', is assembled first.

(2) **RNA-directed DNA polymerase** is the EC recommended name for **reverse transcriptase**.

DNA primase a DNA-directed **RNA polymerase** (EC 2.7.7.–) of the bacterial **primosome**. It associates transiently with the primosome and synthesizes short RNA primers for the **Okazaki fragments** on both template strands at replication forks. Example from *Escherichia coli*: database code PRIM_ECOLI, 581 amino acids (65.49 kDa).

DNA print the pattern formed by denaturing the DNA in colonies of bacteria grown on a support and fixing the DNA to the support.

DNA provirus *see* **provirus**.

DNA repair enzyme any of the various enzymes involved in the different stages of DNA repair. Three steps are involved, each catalysed by a different set of enzymes: (1) the altered portion of DNA is removed by repair nucleases; (2) **DNA polymerase** fills the gap with a complementary copy; (3) the break is sealed by **DNA ligase**. There are two other related repair pathways, called (base-)**excision repair** and nucleotide-excision repair. *See also* **repair enzyme**.

DNA replication *see* **replication of DNA**.

DNA–RNA hybrid a double helix consisting of one DNA chain and one complementary RNA chain, the two chains being held together by hydrogen bonds between the complementary **base pairs**.

DNA–RNA hybridization *or* **DNA–RNA hybridisation** the formation of a **duplex** (def. 2) nucleic-acid structure that occurs when DNA and RNA molecules that have complementary base sequences are brought together. This phenomenon is exploited in a technique used to localize genes in a chromosome that depends on allowing radioactively labelled RNA to hybridize with denatured, single-stranded DNA from which the RNA was transcribed and then determining the position on the DNA where hybridization has taken place by autoradiography. It also forms the basis of **Northern blotting**.

DNase *usual abbr. for* **deoxyribonuclease**. *Compare* **DNAase**.

(DNA) sealase *an alternative name for* **polynucleotide ligase** (def. 1).

DNA sequencing determination of the order in which bases occur in DNA. Usually the DNA is cut with restriction enzymes and subjected to either the **chemical cleavage method** or the **chain-termination method**.

DNA superhelix *see* **supercoil**.

(DNA) swivelase *a former name for* type I **DNA topoisomerase**.

DNA topoisomerase any enzyme that alters superhelix density in supercoiled DNA. Topoisomerases are found in all cell types, from microorganisms to those of humans, and in some viruses e.g. bacteriophage T4 and vaccinia. All topoisomerases isolated so far have the ability to relax negatively supercoiled DNA, converting it to a less supercoiled form. They have been divided into type I, which make a transient single-strand break, and type II, which make a transient double-strand break. **Type I DNA topoisomerase**, EC 5.99.1.2; *other names*: DNA topoisomerase, relaxing enzyme, untwisting enzyme, swivelase, nicking–closing enzyme, ω-protein; it catalyses the ATP-independent breakage of a single strand of DNA, which may be followed by passage (i.e., in the case of duplex DNA, transfer of the unbroken strand through the broken strand) and rejoining. This has the effect of relaxing one negative supercoil. Example from *Escherichia coli*: database code TOP1_ECOLI, 864 amino acids (97.29 kDa). This enzyme can relax only negatively supercoiled DNA, whereas some enzymes, e.g. that from calf thymus, can relax both negatively and positively supercoiled DNA. **Type II DNA topoisomerase**, EC 5.99.1.3; *other name*: DNA topoisomerase (ATP-hydrolysing); it catalyses ATP-dependent breakage, passage (in this case, of a double-strand through a double-strand break) and rejoining of the double-stranded DNA. This enzyme can thus decatenate circular duplex DNA. All type II enzymes can relax both positively and negatively supercoiled DNA. Bacterial **DNA gyrase** is a special example of this class of enzyme. In addition to the properties of the other type II enzymes, it catalyses the ATP-dependent introduction of negative superhelical turns into a closed circular DNA. It is an A_2B_2 tetramer. The energy-free topoisomerase activity of the A subunit, which breaks the DNA, is inhibited by 4-quinolone antibiotics such as nalidixic acid and ciprofloxacin. The energy-transducing activity of the B subunit is inhibited by novobiocin and other coumarin antibiotics. Example, subunit A: database code GYRA_ECOLI, 875 amino acids (96.85 kDa); subunit B: database code GYRB_ECOLI, 803 amino acids (89.72 kDa). The breaking and rejoining of DNA is catalysed by the A subunit; the B subunit is the ATPase. A distinctive property of this particular enzyme is that it can introduce negative superhelical turns into a closed circular DNA molecule with the coupled hydrolysis of ATP. *See also* **linkage number**, **supercoil**, **winding number**, **writhing number**.

(DNA) untwisting enzyme *an alternative name for* **(DNA) swivelase**.

DNA virus *or* **deoxyribovirus** any virus in which the genome consists of DNA, either double-stranded (in class I viruses) or single-stranded (in class II viruses). *See* **Baltimore classification of viruses**.

DNFB *abbr. for* (2,4-)dinitrofluorobenzene. *See* **Sanger's reagent**.

Dnp *symbol for* **dinitrophenyl** group.

DNP *abbr. for* **1** (2,4-)dinitrophenol. **2** deoxyribonucleoprotein (use deprecated).

Dns *symbol for* 5-(dimethylamino)naphth-1-ylsulfonyl; *see also* **dansyl**.

dNTP *abbr. for* any deoxynucleoside (5′-)triphosphate (the deoxynucleoside being either unspecified or unknown).

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DOC *abbr. for* (use discouraged) **1** deoxycholate (*see* **deoxycholic acid**). **2 deoxycorticosterone**.

doca *or* **DOCA** *abbr. for* deoxycorticosterone acetate (*see* **deoxycorticosterone**).

Docetaxel *a proprietary name for* a semisynthetic analogue of **taxol**.

docking the binding of any macromolecule or part of such a molecule to its specific harbouring site on another molecular structure. *See also* **signal recognition particle receptor**.

docking protein *another name for* **signal recognition particle receptor**.

docosa+ *or (before a vowel)* **docos+** *prefix* indicating twenty-two or twenty-two times.

docosadienoic acid any straight-chain fatty acid having 22 carbon atoms and two double bonds. The (5*Z*,13*Z*)-form has been reported to occur in *Limnanthes douglasii*.

docosahexaenoic acid any straight-chain fatty acid having 22 carbon atoms and six double bonds. Only the (all-*Z*)-4,7,10,13,16,19-isomer, of the *n*-3 family, occurs naturally, being present in substantial amounts (10–15% of total fatty acids) in fish oils, and in variable amounts (a few percent of total) in animal glycerophospholipids. It can be formed metabolically from α-linolenic acid.

docosanoic acid *or* **behenic acid** a straight-chain saturated fatty acid having 22 carbon atoms that occurs as a constituent of cerebrosides and some seed oils (especially of *Lophira* spp.); in some of the latter it accounts for 20–30% of total fatty acids.

docosapentaenoic acid any straight-chain fatty acid having 22 carbon atoms and five double bonds. The (all-*Z*)-4,7,10,13,16-isomer is a member of the *n*-6 family and can be formed metabolically from linoleic acid; it is a constituent of animal glycerophospholipids. The (all-*Z*)-7,10,13,16,19-isomer, of the *n*-3 family, can be formed metabolically from α-linolenic acid; it is a precursor of 4,7,10,13,16,19-docosahexaenoic acid, and is present in small amounts (a few percent) in animal glycerophospholipids and in larger amounts (up to 10%) in fish oils.

docosatetraenoic acid any straight-chain fatty acid having 22 carbon atoms and four double bonds. Adrenic acid is found in animal glycerophospholipids, especially in brain and heart of animals fed sunflower or corn oil, and is presumed to be the (all-*Z*)-7,10,13,16-isomer.

docosatrienoic acid any straight-chain fatty acid having 22 carbon atoms and three double bonds. The (all-*Z*)-7,10,13-isomer occurs in animal lipids, especially during essential fatty acid deficiency.

docosenoic acid any straight-chain fatty acid having 22 carbon atoms and one double bond. The (11*Z*)-isomer, cetoleic acid, occurs in marine oils and rapeseed oil. The (13*Z*)-isomer, erucic acid, is an important constituent of rapeseed and other oils of plants belonging to the family Cruciferae. The possibility that it may be harmful has prompted efforts to breed crop varieties that yield oils containing low levels or none of this fatty acid.

Dod *symbol for* the dodecyl group.

dodeca+ *or (before a vowel)* **dodec+** *prefix* indicating twelve.

dodecandrin a type I **ribosome-inactivating protein**.

dodecanoic acid *systematic name for* lauric acid, a straight-chain saturated fatty acid having 12 carbon atoms. *See also* **laurate**.

dodecanoyl *symbol* Lau; *systematic name for* **lauroyl**.

dodecenoic acid any straight-chain fatty acid having 12 carbon atoms and one double bond.

dodecenoyl the acyl group derived from any dodecenoic acid.

dodecenoyl-CoA Δ-isomerase EC 5.3.3.8; *systematic name*: dodecenoyl-CoA Δ^3-*cis*–Δ^2-*trans*-isomerase; *other names*: Δ^3-*cis*-Δ^2-*trans*-enoyl-CoA isomerase; acetylene–allene isomerase; 3,2 *trans*-enoyl-CoA isomerase. An enzyme that is involved in **unsaturated fatty acid oxidation**; it catalyses the isomerization of 3-*cis*-dodecenoyl-CoA to 2-*trans*-dodecenoyl-CoA, thereby producing a substrate for **enoyl-CoA hydratase**. Example from rat: database code S21091, 298 amino acids (32.86 kDa). *See also* **peroxisomal bifunctional enzyme**.

dodecyl *symbol*: Dod; *preferred name for* the alkyl group, CH_3–$[CH_2]_{10}$–CH_2– (*also known as* **lauryl**), derived from dodecane.

***n*-dodecyl-*N*,*N*-dimethylglycine** lauryldimethylbetaine; a zwitterionic betaine detergent, CMC 1.6–2.1 mM. *Proprietary name*: Empigen BB.

***n*-dodecyl-β-D-glucopyranoside** a water-soluble nonionic detergent, CMC 0.13 mM.

***n*-dodecyl-β-D-maltoside** a water-soluble nonionic detergent, aggregation number 98, CMC 0.1–0.6 mM.

dodecylsulfate the CH_3–$[CH_2]_{10}$–CH_2–O–SO_3 anion. *See* **sodium dodecyl sulfate**.

doghouse configuration (of a cyclobutadipyrimidine) *see* **pyrimidine dimer**.

Doisy, Edward Adelbert (1893–1986), US chemist, biochemist, and endocrinologist remembered for the isolation of the female sex hormones estradiol, estriol, and estrone, and especially for his isolation (from putrified fish meal) of a second antihemorrhagic principle named vitamin K_2 (now termed menaquinone) (*see also* **Dam**) and for his subsequent structural characterization of vitamins K_1 and K_2; Nobel Laureate in Physiology or Medicine (1943) 'for his discovery of the chemical nature of vitamin K' [prize shared with H. C. P. Dam].

dolichol *the recommended term for* any 2,3-dihydropolyprenol derived from four or more linked isoprene units, i.e. any prenol derivative of general structure H–[–CH_2–C(CH_3)=CH–CH_2–]$_n$–CH_2–CH(CH_3)–CH_2–CH_2–OH where *n* is greater than 3; in naturally occurring dolichols *n* is commonly in the range 13–23. (*Note*: Because the isoprene unit carrying the hydroxyl group is saturated in dolichols, they are not true **prenols** or **polyprenols**, though often classed as such. It is therefore recommended that, unless qualified, these collective terms are not used to include dolichols.) The phosphoric esters of dolichol (dolichol phosphate *or* phosphodolichol *or* dolichyl phosphate) and the diphosphoric esters (dolichol diphosphate *or* diphosphodolichol *or* dolichyl diphosphate) function in eukaryotes as carriers of mono- and oligosaccharide residues in the glycosylation of lipids and proteins within intracellular membranes. First, glycosyl groups are transferred from soluble nucleoside-diphosphosugars such as GDPmannose, UDP-*N*-acetylglucosamine, UDPglucose, or UDPxylose to form dolichyl phospho- or diphosphosugars. Then dolichyl diphosphooligosaccharides are built up from these by stepwise transfer of additional sugar residues. Finally the completed oligosaccharide moiety is transferred to a lipid or to a growing polypeptide chain with release of dolichyl diphosphate.

dolichol kinase EC 2.7.1.108; an enzyme that catalyses the formation of dolichyl phosphate from CTP and dolichol with release of CDP. Dolichyl phosphate is a precursor of dolichyl diphosphooligosaccharides, dolichyl phosphoglucose, and dolichyl phosphomannose, intermediates in N-linked glycoprotein oligosaccharide biosynthesis. Example from yeast: database code SC59_YEAST, 519 amino acids (58.84 kDa).

dolichol *O*-acyltransferase EC 2.3.1.123; an enzyme that catalyses the formation of dolichyl palmitate from palmitoyl-CoA and dolichol with release of CoA. Acylated dolichols are found in some cell membranes, though their function is obscure.

dolichyl the alkyl group derived from a **dolichol** by loss of its hydroxyl group.

dolichyl diphosphooligosaccharide a precursor for the transfer of N-linked oligosaccharide chains to protein in the synthesis of glycoproteins. It consists of dolichol esterified to diphosphate with an oligosaccharide chain linked to the diphosphate by the C-1 of the sugar at the reducing end of the chain.

dolichyl-diphosphooligosaccharide–protein glycosyl-

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transferase EC 2.4.1.119; an enzyme that catalyses the reaction of dolichyl diphosphooligosaccharide with protein L-asparagine to form a glycoprotein with the oligosaccharide chain attached by glycosylamine linkage to protein L-asparagine, with release of dolichyl phosphate. Example from chicken: database code GSBP_CHICK, 508 amino acids (56.90 kDa).

dolichyl-phosphate β-D-glucosyltransferase EC 2.4.1.117; an enzyme that catalyses the reaction of UDPglucose with dolichyl phosphate to form dolichyl β-D-glucosyl phosphate (an intermediate in the biosynthesis of N-linked glycoprotein oligosaccharides) and UDP. It is a type II membrane protein of the endoplasmic reticulum involved in the glycosylation pathway. Example from yeast: database code ALG5_YEAST, 334 amino acids (38.30 kDa).

dolichyl-phosphate-mannose–protein mannosyltransferase EC 2.4.1.109; an enzyme that catalyses the reaction of dolichyl phosphate D-mannose with protein to form *O*-D-mannosylprotein and dolichyl phosphate. Two examples from yeast: database code PMT1_YEAST, 817 amino acids (92.57 kDa); and database code PMT2_YEAST, 758 amino acids (86.75 kDa). *See also* **dolichyl-phosphate β-D-mannosyltransferase**.

dolichyl-phosphate β-D-mannosyltransferase EC 2.4.1.83; an enzyme that catalyses the formation of dolichyl D-mannosyl phosphate, an intermediate in the biosynthesis of N-linked glycoprotein oligosaccharides, from GDPmannose and dolichol phosphate with release of GDP. Example (precursor of isoenzyme I) from yeast: database code DPM1_YEAST, 267 amino acids (30.33 kDa). *See also* **dolichyl-phosphate-mannose–protein mannosyltransferase**.

domain **1** any topological region having specific characteristics, contained within certain limits, and/or under individual control. **2** *or* **structural domain** a compact, globular region in the structure of a single protein molecule, which may consist of several such globular regions held together by more flexible parts of the polypeptide chain. It has been suggested that the word be reserved for large subassemblies that would be stable if the polypeptide chain connecting them to the rest of the protein molecule were to be cleaved and that the term **folding unit** be used to define small assemblies of secondary structure segments in a protein molecule. **3** a region of a protein molecule delimited on the basis of function without knowledge of and relation to the molecular substructure, as, e.g., the part of a protein molecule that binds to a receptor, that binds a substrate and possesses a catalytic function forming a **catalytic domain**, or that, in a membrane protein, passes through the membrane from one face to the other, forming a **transmembrane domain**. Such a region may contain more than one structural domain (*see* def. 2) **4** a poorly characterized length of chromosomal DNA, of the order of 50–200 kilobase pairs, that comprises all the (coding or noncoding) sequences required for the formation of mRNA for any one (specified) protein. **5** a zone within a cellular membrane consisting of one class of component, e.g. lipid. **6** a diverse set of cellular events, processes, and metabolic reactions controlled or affected by a specific agent, e.g. a hormone or another messenger. *See* **metabolic code**. **7** a mathematical aggregate to which a variable is confined. **8** *(in physics)* any region in a ferromagnetic solid in which all the atoms have the spins of their unpaired electrons aligned in the same direction: **magnetic domain**. *See also* **Appendix E.**

domain of bonding the two linked **binding sets** through which a pair of associated **protomers** are associated.

dominant *(in genetics)* describing a gene that produces the same character whether present in the homozygous state or in the heterozygous state (i.e. together with a different specified allele). The ineffective heterozygous allele is described as **recessive** to the dominant one. Dominant inherited diseases fall into one of three categories: (1) '**change of function**' in which the abnormal protein acquires a novel activity that is deleterious to the cell, (2) '**dominant negative**' in which the abnormal protein forms heterooligomeric complexes with the protein from the normal allele thereby knocking out the function of the entire protein complex, (3) '**haplo-insufficiency**' in which a single copy of the gene has lost function and the 50% of the normal amount of protein that is produced from the non-mutated allele is not adequate to preclude clinical symptoms. Examples: type (1), sodium channel disorders; type (2), mutations in collagen genes which lead to osteogenesis imperfecta; type (3), loss of function in one copy of the low-density-lipoprotein receptor gene resulting in familial hypercholesterolemia.

Donnan effect *or* **Donnan (membrane) equilibrium** the effect of the presence of charged macromolecules upon one side of a semipermeable membrane on the distribution of small, permeable ions across the membrane. At equilibrium, the small counterions will be more concentrated on the macromolecules' side of the membrane and the small ions of the same charge as the macromolecules will be less concentrated there, whereas on the side of the membrane with no macromolecules the concentrations of the small ions of opposite charge will be equal. It can be shown that, if the small ions are A^+ and B^-,

$$[A^+]_{(1)}/\,[A^+]_{(2)} = [B^-]_{(2)}/\,[B^-]_{(1)} = r_D,$$

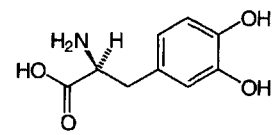
where r_D is the **Donnan ratio** and the subscripts 1 and 2 indicate the two sides of the membrane. [After Frederick George Donnan (1870–1956), British physical chemist.]

donor *(in chemistry)* any chemical species that is able to donate one or more electrons, atoms, or groups to another species, the acceptor.

donor atom **1** an atom that supplies two electrons in forming a **dipolar bond.** **2** an atom, added as an impurity to a semiconductor, that provides additional electrons in the conduction band. *See also* **electron donor**.

donor cell any living cell that contributes genetic information to another, **recipient** cell. *See* **conjugation** (def. 3), **transduction**, **transformation**.

dopa *or* **DOPA** *abbr. for* 3-hydroxytyrosine; 3,4-dihydroxyphenylalanine; 2-amino-3-(3,4-dihydroxyphenyl)propanoic acid; the naturally occurring enantiomer is 3-hydroxy-L-tyrosine (*abbr.*: L-dopa, also known as levodopa because it is levorotatory; $[\alpha]_{546}^{20} \approx 13.0$). L-Dopa is formed from L-tyrosine by tyrosine 3-monooxygenase, EC 1.14.16.2, and is an immediate metabolic precursor of the neurotransmitter **dopamine** and other **catecholamines**. L-Dopa is used in the treatment of **Parkinson's disease**.



dopac *or* **DOPAC** *abbr. for* dihydroxyphenylacetate.

dopachrome Δ-isomerase EC 5.3.3.12; *systematic name*: dopachrome Δ^7–Δ^2-isomerase; an enzyme that catalyses the conversion of dopachrome (2-carboxy-2,3-dihydroindole-5,6-quinone) to 5,6-dihydroxyindole-2-carboxylate. Dopachrome is formed non-enzymatically from dopaquinone, the product of **monophenol monooxygenase**. These are reactions in the pathway of melanin synthesis. A deficiency in the enzyme results from a mutation in mice known as ***slaty***. The enzyme contains zinc. Example from *Mus musculus*: database code TYR2_MOUSE, 517 amino acids (58.57 kDa).

dopa decarboxylase *see* **aromatic-L-amino-acid decarboxylase**.

dopamine *an alternative name for* 3,4-dihydroxyphenylethylamine; 3-hydroxytyramine; 3,4-dihydroxyphenylethylamine; 4-(2-aminoethyl)-1,2-benzenediol; a **catecholamine** neurotransmitter formed by aromatic-L-amino-acid decarboxylase, EC 4.1.1.28, from 3,4-dihydroxy-L-phenylalanine. A metabolic

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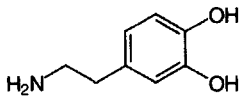
precursor of **norepinephrine** and **epinephrine**, it is found in **dopaminergic** nerves in the brain and in the adrenal medulla. *See also* **Parkinson's disease**.



dopamine β-hydroxylase EC 1.14.17.1; *recommended name*: dopamine β-monooxygenase; *systematic name*: 3,4-dihydroxyphenethylamine,ascorbate:oxygen oxidoreductase (β-hydroxylating). An enzyme that catalyses hydroxylation of dopamine to norepinephrine in aminergic neurons releasing norepinephrine and epinephrine; ascorbate is simultaneously oxidized to dehydroascorbate. The enzyme is a copper protein, stimulated by fumarate. It is absent from dopaminergic neurons. Example, homotetramer, human precursor, database code DOPO_HUMAN, 603 amino acids (67.62 kDa).

dopamine β-monooxygenase *see* **dopamine β-hydroxylase**.

dopamine receptor any of several membrane proteins that bind dopamine and mediate its intracellular effects. Types D_1 to D_5 have been recognized; D_1 and D_5 (also called D_{1A} and D_{1B}) comprise one subfamily; D_2, D_3, and D_4 (also called D_{2A}, D_{2B}, and D_{2C}) comprise a second subfamily. D_3 receptors seem to be insensitive to guanine nucleotides and regulate conductance of Ca^{2+}. All are seven-transmembrane-domain receptors that couple to G-proteins. D_1 and D_5 elevate cyclic AMP, but vary in binding characteristics; D_2 has a short and a long form originating from alternative splicing; in humans, the short form (D_{2S}) has 414 amino acids, and the long form (D_{2L}) has 443 amino acids. D_2 lowers cyclic AMP levels and regulates ion channels, opening K^+ and inhibiting Ca^{2+} channels. D_3 and D_4 have binding characteristics similar to, but distinct from D_2; their action is not mediated by G-protein interaction with adenylate cyclase. Examples, all human; D_1: database code DADR_HUMAN, 446 amino acids (49.29 kDa); D_2: database code D2DR_HUMAN, 443 amino acids (50.62 kDa); D_3: database code D3DR_HUMAN, 400 amino acids (44.22 kDa); D_4: database code D4DR_HUMAN, 387 amino acids (40.89 kDa); D_5: database code DBDR_HUMAN, 477 amino acids (52.95 kDa).

dopaminergic describing a nerve that is activated by dopamine. The term is applied to nerves that act by releasing dopamine at their nerve endings. *Compare* **adrenergic**, **aminergic**, **cholinergic**, **peptidergic**, **purinergic**, **serotonergic**.

Doppler effect the apparent change in the frequency of acoustic or electromagnetic waves due to relative motion between the source and the observer. The frequency appears to increase when the source and the observer move towards each other, and to decrease when they move away from each other. [After Christian Johann Doppler (1803–53), Austrian mathematician and physicist.]

dorsal protein embryonic developmental morphogenetic nuclear protein; a protein whose concentration in the nucleus of a cell during the blastoderm stage of development determines the cell's lateral or ventral identity. It is similar to the product of the vertebrate proto-oncogene *c-rel*. Example from *Drosophila melanogaster*: database code DORS_DROME, 678 amino acids (75.39 kDa).

dose **1** a measured quantity of a drug, microorganism, radiation, etc. administered to an organism, often at specified intervals. In experimental pharmacology, the units and routes of administration should be specified and the quantity of the drug expressed per unit of animal mass, e.g. mol kg^{-1}, mg kg^{-1}, mg min^{-1} kg^{-1}. **2** to prescribe or administer a dose or doses. — **dosage** *n.*

dose equivalent *symbol: H*; a measure of the biological effects of **ionizing radiation** upon humans (or other mammals) used in radiation dosimetry and health physics. It is usually equal to the **absorbed dose** multiplied by the **quality factor**. In the case of radiation arising from radioactive material within a person's body, the absorbed dose must be multiplied also by a distribution factor (normally unity, but in certain instances given a value of 5) in order to take account of any nonuniform distribution of radioactivity. The CGS unit of dose equivalent is the **rem**; the corresponding SI derived unit is the **sievert** (def. 1).

dose rate in radiation dosimetry, the amount of **ionizing radiation** (expressed in grays, rads, rems, röntgens, or sieverts) received or receivable by an irradiated object or organism in unit time. For personnel, it is usually expressed in sieverts per hour. (There is no separately named unit of dose rate.)

dose ratio *an older name for* **concentration ratio**.

dose–response curve any graphical representation of the relationship between the size of an administered dose and the extent of the response of the organism, or other test system, to the dose. The response may be some biochemical or physiological change in one or more organisms, tissue samples etc., or the proportion of organisms in a group that show a response.

dosimeter *or* **dose meter** an instrument for measuring the quantity of ionizing radiation administered to an organism or an object, or the intensity of a source of such radiation.

dosimetry the process of measuring administered quantities of ionizing radiation, drugs, microorganisms, etc.

dot hybridization *or* **dot hybridisation** *or* **dot blotting** a development of **blotting** or blot transfer, in which as little as 1 pg of a specific nucleic-acid sequence, bound to nitrocellulose as a small spot, can be detected using a ^{32}P-labelled probe as a 'dot blot'.

double-antibody method any technique in which a specific antibody, used to detect or measure its corresponding antigen, as in **immunoassay**, is isolated from the reaction mixture by combination with heterologous antibody to the specific antibody. *Compare* **antiglobulin test**.

double-beam spectrophotometer a **spectrophotometer** in which the incident light beam is split into two halves, one half passing through the sample and the second half passing through the reference so that direct measurement of the difference in absorption can be made. In one type the two emergent beams fall on different detectors and the resulting signal is a direct current; in another type the incident beam passes alternately through the sample and the reference, and the two emergent beams fall on the same detector resulting in an alternating current signal.

double-blind testing a method of evaluating the efficacy of a substance (e.g. a drug) in which neither the subjects nor the experimenter knows the identity of the samples at the time of the evaluation.

double bond a **covalent bond** that consists of two electron pairs shared by two atoms.

double-displacement (enzyme) mechanism *or* **ping-pong mechanism** *or* **substituted-enzyme mechanism** any enzymic mechanism in which an enzyme reacts with one substrate to give a covalently modified enzyme together with the release of one product, and the modified enzyme then reacts with the second substrate with the subsequent release of the second product and the return of the enzyme to its initial state.

double helix *or* **Watson–Crick model of DNA**; the main features of this model are that DNA consists of two antiparallel helical polynucleotide chains coiled around the same axis to form a double helix. Deoxyribose–phosphate backbones are on the outside of the helix and purine and pyrimidine bases lie approximately at right angles to the axis on the inside of the helix. The diameter of the helix is 2.0 nm and there is a residue on each chain every 0.34 nm. The angle between each residue on the same chain is 36°, so that the structure repeats after 10 residues (3.4 nm) on each chain. The two chains are held together by hydrogen bonds between pairs of bases, each mem-

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ber of the pair belonging to a different polynucleotide chain. Adenine is always paired with thymine and guanine with cytosine. The two chains are therefore complementary.

double immunodiffusion *or* **double diffusion** a technique of **immunodiffusion** in which both the antibody and the antigen diffuse towards each other through a gel to form lines of precipitation. *See* **Ouchterlony technique**.

double labelling an experimental strategy in which either a single chemical compound is labelled with two different nuclides or two compounds are each labelled with a different nuclide. It is used to follow the simultaneous transformations of two substances or two parts of one substance, or to distinguish identical molecules synthesized at different times. —**doubly labelled** *adj.*

double layer *see* **electric double layer**.

double membrane *see* **unit membrane**.

double-reciprocal plot a plot of $1/x$ versus $1/y$, where x and y are two variables. If the plot of y versus x has the shape of a **rectangular hyperbola** the corresponding double-reciprocal plot will be a straight line. Note: The x and y axes are not the asymptotes of the rectangular hyperbola. The **Lineweaver–Burk plot** is a double-reciprocal plot. *See also* **hyperbolic kinetics curve**.

double refraction *see* **birefringence**.

double refraction of flow *see* **flow birefringence**.

double-sector cell a **cell** (def. 2), used in analytical ultracentrifugation experiments, with two radial sector-shaped cavities, allowing the concentration distribution of a solute in one sector to be related to that of the solvent alone in the other sector: i.e. the second sector provides a reference for the first.

double-sieve hypothesis a hypothesis invoked to account for the unexpectedly low level of error (misreading) observed in protein biosynthesis. According to this hypothesis, the discrete synthetic and hydrolytic sites that exist on certain aminoacyl-tRNA synthetases provide a two-stage stereochemical sorting mechanism – likened in action to a pair of sieves – for the elimination of inappropriate amino acids. The synthetic site first rejects amino acids larger than that genetically specified; the hydrolytic site then preferentially destroys reaction products of amino acids smaller than, or isosteric with, the one specified. The second process has also been termed **editing** or proofreading. Such a mechanism would have particular importance in discriminating between a pair of very similar amino acids such as isoleucine and valine. *Compare* **kinetic proofreading**.

double-stop terminator two consecutive **termination codons** in a molecule of mRNA.

double-stranded *or* **double-strand** describing a **duplex** form of a nucleic acid. *See* **double-stranded RNA**, **duplex DNA**.

double-stranded RNA *abbr.*: dsRNA; a structure that occurs when complementary base sequences in single-stranded RNA form a **duplex** (def. 2). The RNA may fold back on itself to generate an antiparallel duplex structure, known as the stem, with a loop of unpaired bases at the end. The loop and stem together are called a **hairpin**. The two complementary sequences can result from an inverted repeat. *See also* **palindrome**.

doublet 1 any sequence of two nucleotides in a polynucleotide strand. 2 a closely spaced pair of spectral lines or peaks. *Compare* **twin**.

doubling dilution a serial dilution effected so that the concentration in each tube of the particular cell, substance, etc. of interest is half that in the preceding tube of the series.

doubling time the average time taken for the number of cells in a population to double. It will equal the **generation time** only if every cell in the population is able to form two daughter cells and there is no cell lysis.

Dounce homogenizer *or* **Dounce homogeniser** a hand-operated tissue homogenizer, usually of glass, consisting of a ball that is operated as a piston in a tube. The clearance is adjusted to give a fine particle size reduction without damage to cell nuclei or mitochondria. [After Alexander Latham Dounce, US biochemist (1909–).]

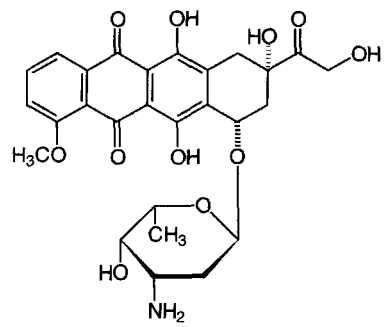
Dowex *proprietary name for* a group of synthetic ion-exchange resins made by Dow Chemical Company. *See also* **cholestyramine resin**.

down regulation 1 a decrease in response of a cell to a hormone brought about either by a decrease in receptor number or by the uncoupling of an effector component. 2 a decrease in the activity of an enzyme or the amount of a protein resulting from the action of an effector molecule on gene expression or protein synthesis. —**down-regulated** *adj.*

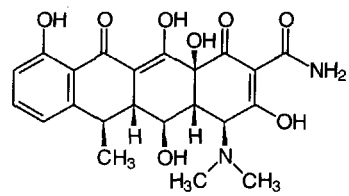
Down's syndrome *or (formerly)* **mongolism** a type of mental abnormality frequently associated with **trisomy** of chromosome 21. The condition is characterized by a small stature, a rounded head with obliquely slanted ('Mongol-like') eyes and high cheekbones, a fissured tongue with enlarged papillae, and a characteristic palmprint. The degree of mental defect varies considerably. [First described in 1866 by John Langdon Haydon Down (1828–96), British physician.]

downstream 1 *(in molecular biology)* that part of a strand of DNA lying towards the 3′ end from the recognition sequence for a particular restriction enzyme. 2 towards the end of a multistage process, or at a stage nearer to the endpoint of the process than a key stage or one under consideration. *Compare* **upstream**.

doxorubicin a cytotoxic anthracycline antibiotic from *Streptomyces peucetius* var. *caesius*; its carbohydrate is **daunosamine**. It intercalates with DNA and prevents the actions of type II **DNA topoisomerase**. It also inhibits reverse transcriptase and acts on cell membranes. It has anti-tumour activity and has been used to treat some forms of cancer.



doxycycline 5-hydroxy-6-deoxytetracycline; an antibiotic having a wide range of activity against both Gram-positive and Gram-negative organisms. It is closely similar to **tetracycline** in structure and mechanism of action. One proprietary name is Vibramycin.



DPG *or* **2,3-DPG** *abbr. for* (2,3-)diphosphoglycerate (former name for **2,3-bis(phospho)-D-glycerate**).

DPG pocket *abbr. for* diphosphoglycerate pocket. *See* **bisphosphoglycerate pocket**.

dpm *or* **d.p.m.** *abbr. for* disintegrations per minute.

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Dpm *see* **A_2pm**.

DPN *abbr. for* diphosphopyridine nucleotide when its oxidation state is unknown or unspecified (obsolete; NAD now used).

DPN$^+$ *abbr. for* diphosphopyridine nucleotide (oxidized) (*obsolete name for* **NAD$^+$**).

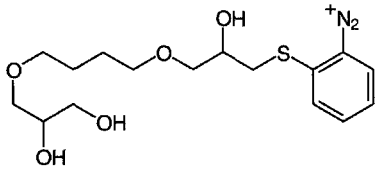
DPNH *abbr. for* reduced diphosphopyridine nucleotide (obsolete; NADH now used).

DPP *abbr. for* dipeptidyl peptidase.

Dpr *see* **A_2pr**.

dps *abbr. for* disintegrations per second.

DPT *abbr. for* 2-diazophenylthioether, *the short name of* the group –O–CH_2–CH(OH)–CH_2–O–[CH_2]$_4$–O–CH_2–CH(OH)–CH_2–S–C_6H_4–N_2^+, used to introduce reactive diazonium groups into cellulose or paper, forming **DPT-cellulose** or **DPT-paper**. These are used in **blot transfer** of proteins or nucleic acids. DPT is formed by diazotization of 2-aminophenylthioether (*abbr.*: APT) groups previously coupled to the support.



D region the (third) hypervariable region occurring between the V region and the J region in the heavy chains (but not in the light chains) of **immunoglobulin** molecules. It is coded for by the D (for 'diversity') gene segment.

dRib *symbol for* the monosaccharide deoxyribose, 2-deoxy-D-ribose.

Drk *abbr. for* **1** a small protein that bears SH2 domains (*see* **SH domain**) and acts as a link between **sevenless** protein and **son of sevenless** protein in the *Drosophila* photoreceptor system (downstream of receptor kinases). **2 Drk1** a mammalian integral membrane protein forming a voltage-dependent potassium channel of the delayed rectifier class. The voltage sensor, probably segment S4, is characterized by a series of positively charged amino-acid residues at every third position. Example from rat: database code CIKA_RAT, 853 amino acids (95.17 kDa).

D-RNA *or* **dRNA** *abbr. for* DNA-like RNA.

dropping-mercury electrode an electrode used in **polarography** in which mercury drops from a reservoir through a capillary tube into the solution under study. It has the advantage of constantly presenting a clean, unpolarized mercury surface to the solution.

Drosophila a genus of small dipterous insects that includes the fruit fly, *D. melanogaster*, also known as vinegar fly or banana fly. This is much used in genetic research because of the giant chromosomes, which occur in the cells of its salivary glands, and because of its short life cycle.

Drude equation an equation describing the variation of optical rotation with wavelength of light. It is useful in the interpretation of measurements of **optical rotatory dispersion**, when it may be expressed in the form:

$$[m']_\lambda = \frac{96\pi N_A}{h\,c} \times \frac{R\lambda_0^2}{\lambda^2 - \lambda_0^2}$$

where N_A is the Avogadro constant, h is the Planck constant, c is the speed of light, R is the rotational strength, λ_0 is the wavelength of the centre of an absorption band, λ is the wavelength of the observation, and $[m']_\lambda$ is the reduced mean residue rotation at that wavelength, as defined at **molar optical rotation**. *See also* **Moffitt–Yang equation**. [After Paul Karl Ludwig Drude (1863–1906), German physicist, noted for, *inter alia*, his work on refraction of light.]

drug any naturally occurring or synthetic substance, other than a nutrient, that, when administered or applied to an organism, affects the structure or functioning of the organism; in particular, any such substance used in the diagnosis, prevention, or treatment of disease.

drug-metabolizing enzyme *or* **xenometabolic enzyme** any enzyme that acts on a drug or other foreign compound but is not known to have any action on a normal metabolite. Many enzymes previously included in this category have subsequently been found to act also on normally occurring substrates.

drug resistance the relatively enhanced resistance of an organism to the action of a drug. It may be caused by induction of an enzyme acting on the drug, by mutation, or by the acquisition of a plasmid coding for drug resistance.

dry ice solid carbon dioxide. It is a convenient cooling agent because, at ordinary atmospheric pressures, heat converts it directly to the gaseous form (sublimation point 194.65 K at 101 325 Pa; –78.5 °C at 760 Torr).

DsbA a 21 kDa protein that is the bacterial functional equivalent in *Escherichia coli* of **protein disulfide-isomerase** in eukaryotes. There is little similarity in the primary structure of the two proteins. The structure of DsbA has been determined by X-ray crystallography and part of the structure shown to be similar to **thioredoxin**.

DSC *abbr. for* differential scanning colorimetry *or* differential scanning calorimeter.

dsDNA *abbr. for* double-strand(ed) DNA (*see* **duplex DNA**).

DSPD *abbr. for* disalicylidenepropanediamine.

dsRNA *abbr. for* double-strand(ed) RNA.

DSS *abbr. for* 2,2-dimethylsilapentane 5-sulfonic acid; a compound used as a water-soluble reference substance in **nuclear magnetic resonance spectroscopy**.

dsx *abbr. for* the *doublesex* gene in *Drosophila melanogaster*. Alternative splicing of the same transcript yields the male-specific protein (database code DSXM_DROME, 549 amino acids (57.35 kDa)); and the female-specific protein (database code DSXF_DROME, 427 amino acids (44.72 kDa)). They are transcription factors that bind to the fat body enhancer.

dT *symbol for* a residue of the deoxynucleoside thymidine (alternative to dThd).

dTDP *abbr. for* deoxyribosylthymine diphosphate *or* thymidine diphosphate, the common names for 2′-deoxyribosylthymine-5′-diphosphate; thymidine 5′-diphosphate; 5′-thymidylyl phosphate; thymine 2′-deoxyriboside 5′-diphosphate.

DTE *abbr. for* 1,4-dithioerythritol.

dThd *symbol for* a residue of the deoxynucleoside thymidine; 2′-deoxyribosylthymine; thymine 2′-deoxyriboside (alternative to dT).

dThd5′*P* *symbol for* thymidine 5′-phosphate.

dThd5′*PP* *symbol for* thymidine 5′-diphosphate (alternative to ppdT).

dThd5′*PPP* *symbol for* thymidine 5′-triphosphate (alternative to pppdT).

dTMP *abbr. for* deoxyribosylthymine monophosphate *or* thymidine monophosphate, the common names for 2′-deoxyribosylthymine 5′-phosphate, thymidine 5′-phosphate, 5′-thymidylic acid, thymine 2′-deoxyriboside 5′-phosphate.

DTNB *abbr. for* 5,5′-dithiobis(2-nitrobenzoic acid); *see* **Ellman's reagent**.

DTT *abbr. for* 1,4-dithiothreitol.

dTTP *abbr. for* deoxyribosylthymine triphosphate *or* thymidine triphosphate, the common names for 2′-deoxyribosylthymine 5′-triphosphate; thymidine 5′-triphosphate; 5′-thymidylyl diphosphate; thymine 2′-deoxyriboside 5′-triphosphate.

dU *symbol for* a residue of the deoxynucleoside 2′-deoxyuridine (alternative to dUrd).

dual specificity mitogen-activated protein kinase kinase *see* **MAP kinase kinase**.

Dubnoff shaker a controlled-temperature water bath with a uniformly oscillating load platform and facilities for main-

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taining a controlled atmosphere. It is used for studies of the metabolism of tissues and microorganisms and for enzyme and blood-coagulation studies. [After Jacob William Dubnoff (1909–), US biochemist.]

Duboscq colorimeter an early, accurate visual colorimeter for determination of small quantities of substances in solution, in which the intensities of colour of two solutions, standard and unknown, were compared by varying the path-lengths of light passing through them from a single source until their apparent colours matched. This was achieved by placing the solutions in flat-bottomed vessels (termed cups) and adjustment of their positions in relation to two identical, fixed, transparent plungers through which the light passed, via prisms, to a divided-field eyepiece. The path-length in each solution was then read from a vernier scale. [After Jules Duboscq (1817–86), French optician.]

Duchenne muscular dystrophy *see* **dystrophin**.

ductless gland *an alternative name for* **endocrine gland**.

dUDP *abbr. for* deoxyuridine diphosphate, the common name for 2′-deoxy-5′-uridylyl phosphate; 2′-deoxyuridine 5′-diphosphate; uracil 2′-deoxyriboside 5′-diphosphate.

Duffy system *symbol*: Fy; a blood-group system for which the antigenic determinant depends on the structure of an erythrocyte membrane glycoprotein, of molecular mass 35–55 kDa, the structural details of which are lacking.

Dulbecco, Renato (1914–), Italian-born US virologist notable for demonstrating how certain viruses are able to transform some cells into a cancerous state; Nobel Laureate in Physiology or Medicine (1975) jointly with D. Baltimore and H. M. Temin 'for their discoveries concerning the interaction between tumour viruses and the genetic material of the cell'.

dulcitol *another (older) name for* **galactitol**.

dUMP *abbr. for* deoxyuridine monophosphate, the common name for 2′-deoxyuridine 5′-phosphate; 2′-deoxy-5′-uridylic acid; uracil 2′-deoxyriboside 5′-phosphate.

duodenum that part of the small intestine extending from the pylorus of the stomach to the jejunum. In mammals it lies around the head of the pancreas and receives the duct from the exocrine pancreas and the gall bladder. —**duodenal** *adj.*

Duolite *proprietary name for* a group of ion-exchange resins. It includes those formerly known by the names Biodeminrolit, De-Acidite, Zeo-Karb, and Zerolit.

duplex **1** having two parts or elements, especially of similar form or function. **2** describing a molecular structure (or part of one) in which two polynucleotide strands lie side by side in a head-to-tail orientation and are linked together along their length; *see* **duplex DNA**. **3** describing a telegraphic system, computer channel, etc. that permits two messages to be sent simultaneously in opposite directions.

duplex DNA double-stranded **DNA** in which the two polynucleotide chains are linked together by hydrogen bonds between complementary **base pairs** along their lengths, with the 3′→5′ phosphodiester bonds of the two chains running in opposite directions. Such a molecule is usually coiled into a double helix and it may or may not be covalently closed into a circular molecule and/or formed into superhelical DNA (*see* **supercoil**) *See also* **double helix**.

duplicate *(in biology)* to reproduce by division into two equal parts; *see* **binary fission**.

duplication *see* **gene duplication**.

dUrd *symbol for* a residue of the deoxynucleoside deoxyuridine; 2′-deoxyribosyluracil; uracil 2′-deoxyriboside (alternative to dU).

dUrd5′*P* *symbol for* deoxyuridine 5′-phosphate.

dUrd5′*PP* *symbol for* deoxyuridine 5′-diphosphate (alternative to ppdU).

dUrd5′*PPP* *symbol for* deoxyuridine 5′-triphosphate (alternative to pppdU).

dUTP *abbr. for* deoxyuridine triphosphate, the common name for 2′-deoxyuridine 5′-triphosphate; 2′-deoxy-5′-uridylyl diphosphate, uracil 2′-deoxyriboside 5′-triphosphate.

dUTPase EC 3.6.1.23; *recommended name*: dUTP pyrophosphatase; *systematic name*: dUTP nucleotidohydrolase; *other name*: deoxyuridine-triphosphatase. An enzyme of nucleotide metabolism in eukaryotes that prevents the incorporation into DNA of deoxyuridylyl residues from dUTP by catalysing the hydrolysis of the latter to dUMP and pyrophosphate. Genes for dUTPase are found in several viruses, e.g. herpes simplex type 1: database code DUT_HSV11, 371 amino acids (39.08 kDa).

Duve *see* **de Duve**.

du Vigneaud, Vincent (1901–78), US biochemist distinguished for the synthesis of the posterior pituitary hormones oxytocin and vasopressin, for establishing the structure of biotin, and for his contributions to the synthesis of penicillin; Nobel Laureate in Chemistry (1955) 'for his work on biochemically important sulphur compounds, especially for the first synthesis of a polypeptide hormone'.

dwarfism underdevelopment of the body due to hyposecretion of **somatotropin**. Affected humans typically attain adult heights of less than 1.25 m.

Dy *symbol for* dysprosium.

dyad **1** two units treated as one. **2** a meiotic chromosome in which the two homologous members of the tetrad have separated. **3** a pair of cells resulting from the first meiotic division. **4** a bivalent atom, molecule, or group. *See also* **dyad symmetry**.

dyad axis a twofold **rotation axis**.

dyad-related describing a phenomenon that occurs at a specific position with respect to a **dyad axis**.

dyad symmetry **1** the type of symmetry occurring in molecular structures in which there is repetition after every 180° rotation around a dyad axis. **2** *(in molecular biology)* the formal description of a palindromic sequence in which the axis of symmetry is at the centre of the palindromic sequence. *See* **palindrome**.

dye a natural or synthetic substance that strongly absorbs certain wavelengths of visible or near ultraviolet light and is used to colour material by becoming firmly attached to it. *See also* **stain**.

dye-exclusion test a test for cell viability based on the phenomenon that living cells exclude some dyes, e.g. Eosin and Trypan Blue, whereas dead cells take them up and become stained.

dye-laser a device for obtaining high-intensity light of chosen wavelength by passing the monochromatic emission beam of a **laser** through a stream of liquid containing a fluorescent dye, and then passing the emitted broad-band fluorescent light through a monochromator. By variation of the dye employed a wide range of wavelengths of high-intensity light can be obtained from the single-wavelength laser emission. The light obtained by this device is necessarily of longer wavelength than that of the laser emission.

dye-ligand chromatography *or* **pseudo-affinity chromatography** *or* **pseudo-ligand affinity chromatography** a technique similar to **affinity chromatography** in which the immobilized ligand is any one of certain reactive dyes (coupled usually to cross-linked agarose), the dye commonly being a triazinyl compound, e.g. Reactive Blue 2 or Reactive Red 120. The technique is thus sometimes referred to (inappropriately) as **triazine-dye affinity chromatography**. The fixed dye molecules selectively bind particular enzyme or other protein molecules; the specificity of the interaction varies widely with both protein and dye, although frequently the dye appears to mimic a natural ligand of the protein. Examples of use are the isolation of nucleotide-requiring enzymes (*see also* **nucleotide-binding fold**) and the removal or purification of albumin from serum. The underlying mechanism is not fully understood but appears to involve both hydrophobic (i.e. apolar) and strongly ionic interactions. Many uses may in reality be examples of **affinity-elution chromatography**.

dynactin the largest protein component of the **dynactin complex**, a 20S multiprotein assembly of total mass about 1.2

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MDa, that activates dynein-based activity *in vivo*. A large structural component of the complex is an actin-like 40 nm filament composed of actin-related protein, to which other components attach. Vertebrate dynactin is a ubiquitously expressed cytoplasmic protein; several isoforms of mass ranging from 117 kDa to 160 kDa are produced by alternative splicing. It has a high degree of homology with the product of the *Drosophila* gene *glued*, essential during embryogenesis, some mutations of which kill homozygous embryos. Example from rat: database code DYNA_RAT, 1325 amino acids (146.05 kDa).

dynamic of, or concerned with, motion or force, or with dynamics.

dynamics **1** the branch of a science, especially mechanics, concerned with the motions of objects and the forces that produce such motions. It includes **kinetics**. **2** those forces that produce change or movement in a system or molecule; the motions (e.g. of residues within a macromolecule) so resulting.

dynamic state of body constituents the phenomenon, discovered in the early 1940s, that body components, especially proteins, are in a state of continuous degradation and resynthesis (i.e. of dynamic equilibrium). It was subsequently found to be applicable to other body constituents, although genomic DNA is a notable exception.

dynamin a microtubule-associated protein able to bind and hydrolyse GTP. The dynamin family includes two types, neuron-specific dynamin 1, and the widely expressed dynamin 2, which exhibit a high degree of sequence similarity in the 300 amino acid N-terminal region containing the GTP-binding site, but show divergence in a 100 amino acid proline-rich C-terminal region that in dynamin 1 but not dynamin 2 is a site for regulation of GTPase activity by phosphorylation–dephosphorylation. Dynamins are activated by protein kinase C and have a **pleckstrin homology domain** which binds acidic (especially inositol-) phospholipids with activation of the GTPase activity. Dynamins are involved in formation of microtubule bundles and in vesicular trafficking; purified dynamin 2 in solution forms helical structures that *in vivo* may facilitate the pinching off of vesicles budding from the plasma membrane and accelerate endocytic recycling. The *Drosophila* protein (a dynamin 2) is a product of *shibire*, a gene known to be involved in endocytosis. Examples, rat dynamin 1: database code DYNI_RAT, 851 amino acids (95.93 kDa); *Drosophila* product of *shibire*: database code DYN_DROME, 883 amino acids (98.54 kDa).

dyne *symbol*: dyn; the CGS unit of force, defined as the force required to give one gram an acceleration of one centimetre per second per second. A gram weight thus represents a force of about 980 dyn. 1 dyn = 10^{-5} N.

dynein a large, multisubunit protein complex with ATPase activity, that is associated with microtubules and functions as a molecular motor to drive the movement of a diverse range of intracellular structures, such as endosomes, lysosomes, and mitochondria, along microtubules towards the centrosome. It is also attached to the peripheral fibrous components of eukaryotic flagella and cilia and is responsible for their movement; it may also play a role in the separation of chromosomes at cell division. The complex consists of two heavy chains (≈500 kDa), three or four intermediate chains (≈70 kDa) and four light chains (≈50 kDa). Example: cytoplasmic dynein heavy chain (MAP-1C) from rat: database code RATDYNEINC, 4644 amino acids, (531 kDa); intermediate chain from *Chlamydomonas reinhardtii*: database code DY06_CHLRE, 567 amino acids (63.52 kDa).

dynorphin an opioid tridecapeptide of high potency found in pig brain, duodenum, and pituitary, having the structure

Tyr-Gly-Gly-Phe-Leu-Arg-Arg-Gln-Phe-Lys-Val-Val-Thr,

the N-terminal pentapeptide sequence of which is identical with **[5-leucine]enkephalin**. It is synthesized as **preprodynorphin** (*also called* preproenkephalin B), from which its precursor protein **prodynorphin** (*also called* β-neoendorphin *or* proenkephalin B), a 236-residue polypeptide, is formed. *See also* **endorphin**.

dys+ *prefix* indicating abnormal, diseased, impaired, painful, or difficult.

dysfunction any abnormality or disturbance in the function of an organ, tissue, cell, or part of a cell. —**dysfunctional** *adj.*

dysgenic genetically deleterious.

dystroglycan a protein precursor yielding a 43 kDa transmembrane glycoprotein and an extracellular 156 kDa dystrophin-associated glycoprotein in skeletal muscle; the 156 kDa component binds **laminin**, acting as a laminin receptor that links the extracellular matrix and **sarcolemma** in skeletal muscle. Example (precursor) from human: database code DSG1_HUMAN, 1049 amino acids (113.59 kDa).

dystrophin a protein present in small amounts in normal muscle but absent or abnormal in patients with **Duchenne muscular dystrophy**. It may play a role in anchoring the cytoskeleton to the plasma membrane. Example from human: database code DMD_HUMAN, 3685 amino acids (426.19 kDa). *See also* **dystroglycan**, **utrophin**.

dystrophin-related protein (*abbr* DRP) *see* **utrophin**.

dystrophy any disorder, sometimes genetic, of the structure and functions of an organ or a tissue, as of muscle or bone. —**dystrophic** *adj.*

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Ee

e *symbol for* **1** electron; it may be written as e^- to indicate its charge; e^+ denotes a positron. **2** *(in mathematics)* the transcendental number equal to the limiting value of the series $[1 + (1/n!)]$ for $n = 1$ to infinity; its value is 2.718 281 828 46. It is used as the base of natural (Napierian) logarithms. **3** equatorial; *see* **conformation**.

e′ *symbol for* pseudo-equatorial; *see* **conformation**.

e *symbol for* **1** elementary charge (or proton charge) **2** efficacy (of a drug).

E *symbol for* **1** a residue of the α-amino acid L-glutamic acid (alternative to Glu). **2** elimination reaction. **3** electromeric effect (in electron displacement). **4** exa+ (SI multiplicative prefix denoting 10^{18}).

$[E]_0$ *or* **$[E]_t$** *or* **$[E]_{stoich}$** *(in enzyme kinetics) symbol for* the total or stoichiometric concentration of active (catalytic) centres.

E_1 *abbr. for* estrone.

E_2 *abbr. for* estradiol.

E74 a protein, expressed during development of *Drosophila*, that correlates with an ecdysone-induced activity of puff 74EF. It is encoded by *Drosophila EIP74Ef*, an ecdysone-inducible gene that encodes two *ETS*-related protein products, E74A and E74B, that differ mainly in their N-terminal regions, and have substantial poly-Ala, poly-Asn, poly-Gln, poly-Gly, and poly-Ser domains.

E *symbol for* **1** *(in chemical nomenclature)* a specific configuration around a double bond; *see* ***E/Z* convention**. **2** electromotive force. **3** electric potential difference (of a galvanic cell). **4** energy; kinetic energy and potential energy may be denoted by the symbols E_k and E_p respectively. **5** extinction coefficient (no longer recommended). **6** *(bold italic)* electric field strength (*see* **electric field**).

(*E*)- prefix *(in chemical nomenclature)* denoting a geometric isomer in which the highest priority ligands according to the Cahn–Ingold–Prelog rules (*see* **sequence rule**) are located on opposite sides of a double bond. *See also* ***E/Z* convention**.

-*E* conformational descriptor denoting the envelope conformation of a monosaccharide or monosaccharide derivative.

E° *or* **$E^{\ominus}$** *symbol for* standard electrode potential.

$E^{\circ\prime}$ *or* **$E^{\ominus\prime}$** *symbol for* standard electrode potential at a specified pH.

E_a *or* **E_A** *symbol for* (Arrhenius) activation energy.

E_{ea} *symbol for* electron affinity (def. 2).

Eadie–Hofstee plot a graphical representation of enzyme kinetic data in which the reaction velocity divided by the substrate concentration, $v/[S]$, is plotted as ordinate against the reaction velocity, v, as abscissa. If a straight line is obtained, the intercept on the abscissa gives the maximum velocity, V, and that on the ordinate V/K_m. The slope is $-1/K_m$. [After George Sharpe Eadie (1895–1976) and Barend Hendrik Jan Hofstee (1912–80). US biochemists, who independently described it in 1942 and 1952, respectively.]

Eagle's medium any of various growth or maintenance media used in tissue culture and essentially comprising a balanced salt solution, usually **Earle's balanced salt solution** or **Hanks's balanced salt solution**, supplemented with amino acids, vitamins, serum, and antibiotics.

EAR-3 *see* **COUP**.

Earle's balanced salt solution a solution used in tissue culture to provide a normal ionic, pH, and osmotic environment for cell growth. It contains, per 100 ml distilled water, 0.68 g NaCl, 0.04 g KCl, 0.02 g $CaCl_2$, 0.02 g $MgSO_4 \cdot 7H_2O$, 0.0125 g $NaH_2PO_4 \cdot H_2O$, 0.22 g $NaHCO_3$, 0.1 g glucose, and 0.002 g Phenol Red; it has a pH of 7.6–7.8.

early enzyme an enzyme that is transcribed from an **early gene** (def. 2) of a virus. *Compare* **late enzyme**.

early gene **1** *or* **immediate gene** any of a number of genes involved in the earliest responses of cells to factors that initiate the transition from quiescence to proliferation. Early genes include those that encode transcription factors, such as the c-*JUN*, c-*FOS*, and c-*EGR* genes, and those coding for structural proteins such as actin. Early genes are further subdivided into immediate-early and delayed-early genes. **2** any viral gene that is transcribed early after the virus infects a host cell. Such genes probably code for proteins that are necessary for viral nucleic acid replication. *Compare* **late gene**.

early growth response protein any of a family of proteins that are expressed early in response to growth factors and function as transcriptional regulators, binding to the DNA sequence 5′-CGCCCCCGC-3′. Example, early growth response protein 1 from human (*other names*: krox24, TF ETR103): database code EGR1_HUMAN, 543 amino acids (57.51 kDa).

early protein a protein that is transcribed from an **early gene** (def. 2) of a virus. *Compare* **late protein**.

early quitter any incomplete polypeptide formed in an *in vitro* translation system.

Easson–Stedman model a model to explain the differences in biological activity of two enantiomeric molecules; it assumes that three of the groups attached to an asymmetric carbon atom in an agonist (or substrate) are involved in its attachment to a specific receptor (or enzyme), one enantiomer will therefore be a better agonist (or substrate) than the other. The concept is similar to, but considerably pre-dates, that developed by Ogston (*see* **Ogston concept**).

EBV *or* **EB virus** *abbr. for* Epstein–Barr virus.

EC *abbr. for* **1** Enzyme Commission; it is used as a prefix in the numerical designation of an enzyme (*see* **enzyme classification**). **2** electron capture. **3** enterochromaffin (as in **EC cell**).

EC_{50} *abbr. for* half effective concentration; the molarity of an agonist that produces 50% of the maximal possible effect of that agonist. Other percentage values (EC_{20}, EC_{40}, etc.) can be specified. The action of the agonist may be stimulatory or inhibitory.

EC cell *abbr. for* enterochromaffin cell.

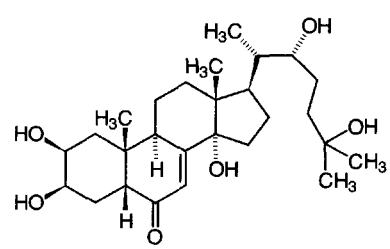
Eccles, (Sir) John Carew (1903–97), Australian neurophysiologist; Nobel Laureate in Physiology or Medicine (1963) jointly with A. L. Hodgkin and A. F. Huxley 'for their discoveries concerning the ionic mechanisms involved in excitation and inhibition in the peripheral and central portions of the nerve cell membrane'.

eccrine **1** describing a secretory cell that discharges its product without loss of cytoplasm. **2** describing a gland made up of such cells. *Compare* **apocrine**, **holocrine**, **merocrine**.

ECD *abbr. for* **1** electron capture detector. **2** electrochemical detection. *See* **polarography**.

ecdysis the periodic shedding of the exoskeleton and construction of a new cuticle, as in insects and crustaceans, or the shedding of the outer layer of the skin, as in reptiles. —**ecdysial** *adj.*

ecdysone **1** **α-ecdysone** (22*R*)-2β,3β,14,22,25-pentahydroxycholest-7-en-6-one; the **ecdysteroid** that is synthesized in and



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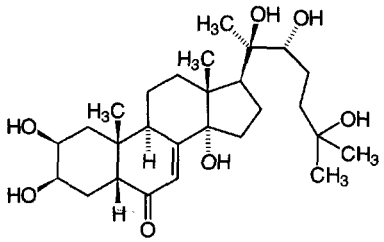
secreted by the prothoracic glands of immature insects and the ovaries of the adult females. First isolated from the silkworm moth (*Bombyx mori*), it is the inactive prohormone of the moulting hormone **ecdysterone**; it may also have intrinsic hormonal activity at other stages of insect development. **2 β-ecdysone** *an alternative name for* **ecdysterone**. **3** *a former name for* **ecdysteroid**.

ecdysone receptor a receptor for ecdysone, located in the cell nucleus and related to the steroid/thyroid/retinoic acid family of nuclear hormone receptors. It consists of a heterodimer of a subunit named EcR (ecdysone receptor) and another named USP (ultraspiracle), the insect homologue of vertebrate retinoid X receptor. The heterodimer binds ecdysone with high affinity, and the ternary complex binds to DNA. Example: database code ECR_DROME, 878 amino acids (93.85 kDa).

ecdysteroid *or (formerly)* **ecdysone** any of a group of polyhydroxylated ketosteroids of which α-ecdysone is the parent substance for the purpose of nomenclature (*see* **ecdysone**). They are almost invariably C_{27} steroids, differing only in the number and/or steric arrangement of their hydroxyl groups. Ecdysteroids are ubiquitous in insects and other arthropods, in which they initiate postembryonic development, including the metamorphosis of immature forms and the development of the reproductive system and the maturation of oocytes in adult females. They have been found also in annelids, molluscs, and nematodes. Cognate substances, often known as **phytoecdysones**, have been identified in plants. The principal ecdysteroids in insects are α-ecdysone (*see* **ecdysone** (def. 1)) and **ecdysterone**.

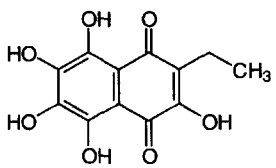
ecdysterone *or* **β-ecdysone** *or* **crustecdysone** *or* **(insect) moulting hormone** 20-hydroxyecdysone; (22*R*)-2β,3β,14,20,22,25-hexahydroxycholest-7-en-6-one; the **ecdysteroid** isolated both from insects and from crustaceans. In insects, ecdysterone is formed in peripheral tissues from **α-ecdysone** through the action of ecdysone 20-monooxygenase (EC 1.14.99.22). The hormone causes puffing of polytene chromosomes, and initiates moulting of larval and pupal forms by stimulating the epidermal cells to enlarge, divide, and secrete degradative enzymes that dissolve the protein and chitin components of the cuticle. Moreover, in the adult females of certain insects, e.g. mosquitoes (*Aëdes* spp.) and *Drosophila melanogaster*, ecdysterone formed from α-ecdysone in the ovaries stimulates vitellogenin synthesis in the fat body.



ECF *abbr. for* extracellular fluid.

ECG *or (US)* **EKG** *abbr. for* **1** electrocardiograph. **2** electrocardiogram.

echinochrome A 2-ethyl-3,5,6,7,8-pentahydroxy-1,4-naphthalenedione; a red pigment of sea urchin eggs.



echinoderm any of the phylum Echinodermata of marine invertebrates that contains sea urchins, sea cucumbers, starfish, etc. They are more or less radially symmetrical, with calcareous skeletal plates in their skin and a well-developed coelom. Locomotion and gaseous exchange are accomplished by means of retractable tube feet. They are related to the same ancestral stock that gave rise to the vertebrates.

eclipsed conformation *see* **torsion angle**.

eclosion hormone any peptide hormone that programmes the death of certain muscles and neurons during metamorphosis of insects.

ecology the branch of biology dealing with the relations of living organisms to their surroundings. —**ecological** *adj.*; **ecologically** *adv.*; **ecologist** *n.*

ecomone any nontrophic molecule that ensures a flux of information between organisms in an **ecosystem**.

ecosystem a unit of the environment together with the organisms it contains. There is a constant interchange between living organisms and their chemical and physical environment.

ecotin a monomeric periplasmic protein of *Escherichia coli* that inhibits the pancreatic serine proteases chymotrypsin, trypsin, and elastases, enabling the organism to survive in the presence of these enzymes. It also inhibits blood coagulation factors Xa and XIIa and kallikrein, thereby having anticoagulant effects. Example from *E. coli*: database code ECOT_ECOLI, 162 amino acids (18.17 kDa).

ECP *abbr. for* eosinophil cationic protein.

ecstasy *see* **3,4-methylenedioxymethamphetamine**.

ECTEOLA cellulose *abbr. for* a weakly basic (pK ≈7.5) anion-exchange material of uncertain structure, prepared by the condensation of epichlorhydrin, triethanolamine (hence e,c + t,e,ola), and cellulose. It is useful for separations of proteins, nucleoproteins, and nucleic acids.

ecto+ *comb. form* indicating external, outer.

ectocrine describing or relating to a metabolite that, when released from the organism in which it was made, differentially affects other organisms of the same or a different species. Such a metabolite might be harmful to some members of a community and beneficial to others. The term includes **allomone**, **ectohormone**, **kairomone**, and **pheromone**. *Compare* **endocrine** (def. 1), **exocrine** (def. 1).

ectoenzyme any enzyme that is attached to the external surface of the plasma membrane of a cell.

ectohormone any **ectocrine** substance whose production and release benefits either the organism producing it or other members of the same species. *Compare* **endohormone**.

ectoparasite any **parasite** that lives on the exterior of its host organism.

ectopic occurring in an unusual place or in an unusual form or manner. For example, an **ectopic protein** is a protein produced by a neoplasm derived from a tissue that does not normally produce that protein. An example is the production of **vasopressin** and **corticotropin** by small cell lung cancer. Ectopic pregnancy occurs when the fertilized ovum implants outside the uterus e.g. in a fallopian tube. *Compare* **entopic**.

ectoplasm the outer, relatively rigid part of the **cytoplasm**. *Compare* **endoplasm**. —**ectoplasmic** *adj.*

ectoplast the part of the plasma membrane of a plant cell that is in contact with the cell wall.

ectoprotein any individual protein found on the exterior of cells. Such proteins may function, e.g., as mediators of cell–cell or cell–surface interactions, or as receptors for substances with regulatory actions on cells.

ectosymbiont a partner in a symbiotic relationship that remains outside the tissues and cells of the other partner, often occupying a body cavity; e.g. one of the cellulose-metabolizing microorganisms occurring in the digestive tract of ruminants. *Compare* **endosymbiont**. *See also* **symbiosis**.

ED_{50} *abbr. for* median effective dose; i.e. the dose of a drug or other agent that produces, on average, a specified all-or-none response in 50% of a test population, or, if the response is

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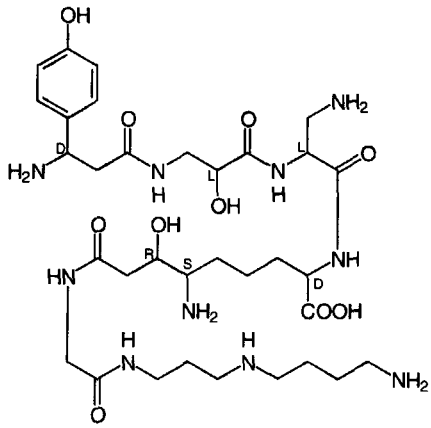
graded, the dose that produces 50% of the maximal response to that drug or agent.

edeine any of several pentapeptide-amide antibiotics elaborated by a strain of *Bacillus brevis* and effective against Gram-positive and Gram-negative bacteria, some fungi and other eukaryotic cells, and some neoplastic cells. Edeine A_1, N^{α}[(N^2-{N^2-[N-(β-tyrosyl)isoseryl]-2,3-diaminopropionyl}-2,6-diamino-7-hydroxyazela-9-yl)glycyl]spermidine, and its N^{ω}-amidinospermidine analogue, edeine B_1, are highly active; their respective constitutional isomers, edeines A_2 and B_2, have low intrinsic activity. In intact bacteria, low concentrations of edeine reversibly inhibit DNA synthesis and enhance RNA synthesis but do not affect protein synthesis. In cell-free systems, edeine A_1 interacts with both ribosomal subunits (preferentially the smaller one) and strongly inhibits translation.



edeine A_1

Edelman, Gerald Maurice (1929–), US biochemist; molecular biologist, and neuroscientist; Nobel Laureate in Physiology or Medicine (1972) jointly with R. R. Porter 'for their discoveries concerning the chemical structure of antibodies'.

edema *or (esp. Brit.)* **oedema** swelling of an organ or tissue due to the accumulation of fluid. —**edematous** *or (esp. Brit.)* **oedematous** *adj.*

edestin a 300 kDa globulin obtained from hemp seed, castor-oil beans, and certain other seeds. It readily forms polymorphic crystals and will support the growth of animals in the absence of other dietary proteins. [From Greek *edestos*, edible.]

edetate *see* **EDTA**.

EDF *abbr. for* erythroid differentiation protein; *see* **activin**.

editing **1** the process or act of altering or adapting erroneous molecular structures, especially nucleotide sequences in polynucleotides, so as to preserve fidelity in the transfer and expression of genetic information. For example, the 3′→5′ exonuclease activity of DNA polymerase I has an editing function in DNA polymerization by removing mismatched residues at the primer terminus of the growing chain. Another editing function is shown by aminoacyl-tRNA synthetases. In the presence of ATP and the 'wrong' amino acid, these enzymes do not catalyse the formation of the incorrect aminoacyl-tRNA but act as ATP pyrophosphatases, hydrolysing ATP to AMP and pyrophosphate. The term is applied also to the processes of conversion of RNA precursors, e.g. hnRNA, to the mature form, mRNA. **2** the insertion, deletion, or substitution of nucleotides within nascent RNA transcripts to produce RNA molecules with sequences that differ from those coded genomically. Most examples have been found in organelle-encoded RNAs, e.g. mitochondrial RNAs, and include ApoB, several **glutamate receptor** mRNAs, and **Wilms tumour** susceptible gene mRNA. In the case of ApoB, a cytidine residue is deaminated to a uridine residue so that the codon for glutamine (CAA) becomes a stop codon (UAA); hence, translation results in a shortened form of the protein.

editosome a macromolecular complex involved in the editing of RNA transcripts. Specific ribonucleotide complexes include guide RNA (*see* **gRNA**), which specifies the edited sequence.

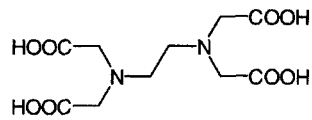
Edman degradation a procedure used in sequencing (poly)peptides in which amino-acid residues are removed stepwise from the N terminus by reaction with phenylisothiocyanate, C_6H_5–N=C=S, to form the phenylthiocarbamyl-peptide (*abbr.*: PTC-peptide). This is then cleaved in anhydrous acid (which favours attack by the sulfur atom on the carbonyl carbon of the terminal peptide) to give a thiazolinone intermediate and the release of the remainder of the peptide chain. The thiazolinone intermediate is hydrolysed to the phenylthiocarbamyl derivative of the N-terminal amino acid, which then cyclizes to form the phenylthiohydantoin derivative (*abbr.*: PTH-amino acid). The PTH-amino acid is extracted into organic solvents and identified by chromatography. These derivatives have a strong UV-absorption at about 259 nm, which permits them to be visualized against a fluorescent screen using an ultraviolet light source. As the remainder of the peptide chain is liberated intact, the procedure may be repeated – up to about ten amino-acid residues may be sequenced in this way, or more in favourable cases. The procedure may be automated, e.g. in a **sequenator**. [After Pehr Victor Edman (1916–77), Swedish protein chemist, who described the method in 1956.]

Edman reagent phenylisothiocyanate; C_6H_5–N=C=S. *See* **Edman degradation**.

EDR *abbr. for* equi-effective dose ratio.

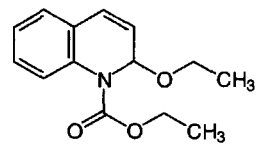
EDRF *abbr. for* endothelium-dependent releasing factor (*see* **nitric oxide**).

EDTA ethylenediaminetetraacetate; edetate; any anion or salt, esp. the (hydrated) disodium salt, of edetic acid, ethylenediamine-*N*,*N*,*N*′,*N*′-tetraacetic acid, (ethylenedinitrilo)tetraacetic acid. Commonly used as the disodium salt, it is a powerful chelating agent for divalent metal ions.



ethylenediaminetetraacetic acid

EEDQ *abbr. for* *N*-ethoxycarbonyl-2-ethoxy-1,2-dihydroquinoline; an agent for peptide condensation that causes little or no racemization; it is useful in coupling ligands to insoluble polymers. It also causes progressive and irreversible inhibition of mitochondrial F_1-ATPase.



eEF-2 a eukaryotic **elongation factor** that is equivalent to the prokaryotic **EF-G**.

EET *(formerly) abbr. for* epoxyeicosatetraenoate.

EF *abbr. for* elongation factor.

EF-1 *see* **EF-T, elongation factor**.

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EFE *abbr. for* ethylene-forming enzyme.

effective dose *see* **ED_{50}**.

effective theoretical plate number *symbol*: N; a number indicative of chromatographic column performance when resolution is taken into account: $N = 16R_s^2/(1-\alpha)^2$, where R_s is the peak resolution and α the separation factor (i.e. the ratio of the distribution ratios or coefficients for the two substances being resolved when measured under identical conditions); by definition α is greater than unity. *Compare* **height equivalent to an effective theoretical plate**. *See also* **theoretical plate**.

effectomer the part of a two-component agonist that brings about the biological effect but only when bound to a **haptomer**, which enables it to interact with the cell membrane and exert its toxic action on intact cells. For example, the A fragment of diphtheria toxin can only exert its toxic effects on a target cell when bound to the B fragment.

effector **1** *or* **modifier** *or* **modulator** *(in molecular biology)* any small molecule or ligand that interacts with an enzyme thereby changing its catalytic behaviour but that is not itself changed during the enzyme action. A **positive effector** enhances catalytic activity while a **negative effector** reduces it. *See also* **allosteric effector**. **2** *(in physiology)* a cell or organ that produces a physiological response when stimulated by the nervous system.

effector site *or* **regulatory site** any site on an enzyme molecule that binds an **effector**.

efferent **1** conveying outwards from a part, organ, or centre; e.g. of a blood vessel, nerve, or duct. **2** an efferent part, e.g. a blood vessel or nerve. *Compare* **afferent**.

efficacy *symbol*: e; a quantitative index of drug action related to the magnitude of a tissue response generated at a given level of receptor occupancy with (full) agonists (of high efficacy) generating the maximum possible response. Drugs with lower efficacy that cannot generate a maximal response even when all receptors are occupied are known as **partial agonists**; **antagonists** have an efficacy of zero. The overall response to a drug will be a function of its efficacy and receptor binding affinity, which determines the proportion of receptors occupied at a given concentration of drug. It may be formulated as the combination of an agonist with its receptors that results in a signal or a **stimulus**, S, equal to the product of the efficacy of the agonist, e_A, and the proportion of receptors occupied, P_{AR}; i.e. $S_A = e_A P_{AR}$. *See also* **intrinsic efficacy**, **maximal agonist effect**.

efficiency the ratio of the useful output of a machine, device, system, etc. to the input, whether in terms of thermal, mechanical, or radiation energy, or of biological or chemical conversions.

efficiency of counting *see* **counting efficiency**.

efficiency of plating *abbr.*: EOP; a quantification of the relative efficiencies with which different cells can be infected by viruses, and support viral replication. It is the ratio of the plaque count to the number of virions in the inoculum.

efflux *see* **flux**.

EF-G *or* **translocase** *abbr. for* an **elongation factor** of *Escherichia coli* that promotes the GTP-dependent translocation of the nascent protein chain from the A-site to the P-site of the ribosome. Database code EFG_ECOLI, 703 amino acids (77.36 kDa). An equivalent factor in eukaryotes is named eEF-2.

EF-hand a **helix-turn-helix** motif that binds Ca^{2+}; it is found in many Ca^{2+}-binding membrane proteins and also in certain others, e.g. **myosin** light chain. It was first recognized in parvalbumin, in which it involves helices E and F. To envisage the motif, use the right hand with thumb and forefinger extended at ≈90° with the remaining three fingers clenched. The thumb will then point towards the C terminus of helix F and the forefinger will point along helix E in the N-terminal direction, the clenched fingers tracing the course of the E–F loop about the bound calcium ion. Two apposed right-hands, representing the E and F and the C and D helices of the molecule, are related by a 2-fold axis of symmetry.

efrapeptin *or* **efrastatin** *or* **A23871** a hydrophobic peptide fungal antibiotic that inhibits oxidative phosphorylation by binding to the soluble component, F_1, of mitochondrial **H⁺-transporting ATP synthase**.

EF-T *or* **transfer factor** a cytoplasmic protein of *Escherichia coli* and other prokaryotes which functions in protein synthesis to promote the GTP-dependent binding of aminoacyl-tRNAs to the A-site of the ribosome during protein chain elongation. EF-T can be dissociated into two polypeptides, EF-Tu (EF-1A) and EF-Ts (EF-1B), the complex being the main form in bacterial cells. These are so described since on their initial isolation one was heat-labile, or unstable, (Tu) and one was heat-stable (Ts). Only Tu functions directly in the GTP-dependent binding of the aminoacyl-tRNA to the A-site of the ribosome but Ts is required for regenerating Tu·GTP after the binding reaction which results in the hydrolysis of GTP to GDP. The factors were originally isolated from both *E. coli* and *Pseudomonas fluorescens*. The structures from *E. coli* are known, database code EFTS_ECOLI, 283 amino acids (30.39 kDa), EFTU_ECOLI, 393 amino acids (43.13 kDa). The 3-D structure of Tu shows high alpha-helix content with identified binding sites for GTP and aminoacyl-tRNA. The Tu from *E. coli* is also a subunit of RNA polymerase of phage Qβ (Q beta). *See also* **elongation factor**.

EF-Ts *now designated* **EF-1B**; *see* **EF-T**.

EF-Tu *now designated* **EF-1A**; *see* **EF-T**.

egasyn an amphipathic glycoprotein, found in microsomal (i.e. endoplasmic reticulum) membranes of mouse liver, that forms a complex with microsomal (but not lysosomal) β-D-glucuronidase (EC 3.2.1.31) and thereby anchors it to the microsomal membranes. It may similarly anchor other polar proteins. It hydrolyses carboxylic esters to an alcohol and carboxylic anion. It has a C-terminal consensus sequence, HXEL, that retains the proteins in the endoplasmic reticulum. Example from *Mus musculus*: database code A55281, 562 amino acids (61.51 kDa). [From e (endoplasmic) + g (glucuronidase) + Greek *syn*, with.]

EG cell *or* **L cell** an **enteroglucagon**-producing endocrine cell. Such cells are found in the basal part of the mucosal glands in the lower intestine; the highest concentrations occur in the terminal ileum and colon. They contain large, dense, secretory granules and are easily distinguishable from other endocrine cells in the same area.

EGF *abbr. for* epidermal growth factor.

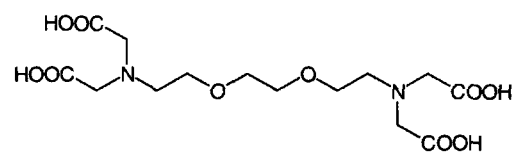
egg the reproductive structure of certain animals, e.g. reptiles, birds, and insects, consisting of an **ovum** together with nutritive and protective tissues, and from which, when fertilized, a young offspring emerges.

egg albumin *the common name for* **ovalbumin**.

egg cell *an alternative name for* **ovum**.

egg white the white part of an egg (especially a bird's egg) surrounding the yolk. Its principal organic constituent is egg albumin (*see* **ovalbumin**).

EGTA *abbr. for* ethylene glycol-*O*,-*O*′-bis(2-amino-ethyl)-*N*,*N*,*N*′,*N*′-tetraacetic acid, [ethylenebis(oxyethylenetrinitrilo)]tetraacetic acid; also for any anion or salt thereof. It is a chelating agent with a high affinity for Ca^{2+} ions.



Ehlers–Danlos syndrome a heterogeneous group of inherited human disorders sharing many phenotypic features. Classically the clinical picture includes hyperelastic, fragile skin, poor wound healing, hyperextensible joints, and easy bruising. Seven distinct genetic forms have been described. Type I,

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which is severe, is inherited as an autosomal dominant; the biochemical lesion is unknown. Types II and III are inherited as autosomal dominants; the biochemical lesions are unknown. Type IV is inherited as an autosomal dominant, but X-linked inheritance is not excluded; patients lack type III collagen and analysis has shown that skin collagen from these patients lacks a peptide of about 100 amino-acid residues that is characteristic of type III collagen. Type V shows X-linked inheritance and fibroblast cultures from a patient show a diminished lysyl oxidase activity, both in the cells and the medium. Type VI is inherited as an autosomal recessive, and collagen from such patients is deficient in hydroxylysine; fibroblast cultures from these patients contain an abnormal lysyl hydroxylase (EC 1.14.11.4). Type VII is presumed to be inherited as an autosomal recessive and the biochemical lesion is a deficiency of procollagen peptidase, with a consequent failure to normally convert procollagen to collagen. [After Edvard Ehlers (1863–1937), German dermatologist, and Henri Alexandre Danlos (1844–1932), French dermatologist, whose respective descriptions of the disorders were published in 1901 and 1908.]

Ehrlich, Paul (1854–1915), German medical scientist famous for his work in chemotherapy, especially for his demonstration of the efficacy of synthetic arsenicals in spirochaetal infections, and notable also for his studies of the interaction of dyes with living tissues, for his work on the assay of antisera, and for advancing the side-chain theory of immunity; Nobel Laureate in Physiology or Medicine (1908) jointly with I. I. Mechnikov 'in recognition of their work on immunity'.

Ehrlich's reagent a solution of *p*-dimethylaminobenzaldehyde in conc. HCl. It forms coloured complexes with a number of compounds, such as indoles, aromatic amines, ureides, and hydroxyproline, and is useful in the detection and estimation of these compounds.

EIA *abbr. for* enzyme immunoassay.

eicosa+ *or (before a vowel)* **eicos+** *a variant spelling (esp. US) of* **icosa+** (*comb. form* denoting twenty or twenty times). This spelling is universally used in naming **eicosanoids**, although not officially recommended (but *see* **Appendix B**).

eicosadienoic acid any straight-chain fatty acid having twenty carbon atoms and two double bonds per molecule. The *all-Z*-(8,11)-isomer is a normally minor metabolite of oleic acid in mammals, but is important as an intermediate in the pathway synthesizing *all-Z*-eicosa-5,8,11-trienoic acid (**Mead acid**) during essential fatty acid deficiency. The (5,11)-isomer occurs in gymnosperms, and several others have been synthesized. The (11*Z*,14*Z*)-isomer occurs as an intermediate in the synthesis of arachiodonate from linoleate via dihomo-γ-linolenate, but this is not the major pathway for this biosynthesis.

eicosanoic acid *the systematic name for* **arachidic acid**.

eicosanoid any of various agents that are C_{20} polyunsaturated fatty acids, commonly arachidonic acid (*see* **eicosatetraenoic acid**), or an **eicosapentaenoic acid**, or their skeletal derivatives. They include the **leukotrienes** and the **prostanoids** and are noted for their widespread biological activity, such as contraction or relaxation of smooth muscle, platelet aggregation, and the inflammatory response.

eicosapentaenoic acid any straight-chain fatty acid having twenty carbon atoms and five double bonds per molecule. The most noteworthy is the *all-Z*-(5,8,11,14,17)-isomer, which occurs in animal phospholipids, especially those of many marine species; fish oils are a good source, with eicosapentaenoic acids often representing up to 10% of total fatty acids. Eicosapentaenoic acids act as precursors of the PG_3 series of **prostaglandins**. The suggestion has been made that a higher than normal content of this acid in the diet can protect against heart disease.

eicosatetraenoic acid any straight-chain fatty acid having twenty carbon atoms and four double bonds per molecule. The *all-Z*-(5,8,11,14)-isomer is **arachidonic acid**. The (8,11,14,17)-isomer is an important intermediate in the formation of long-chain *n*-3 fatty acids from (9,12,15)-linolenic acid, being formed from that acid by desaturation at C-6 and chain elongation. The (5,11,14,17)-isomer is another naturally occurring form.

eicosatetraynoic acid any straight-chain fatty acid having twenty carbon atoms and four triple bonds per molecule. eicosa-5,8,11,14-tetraynoic acid (*abbr.*: ETYA) is a relatively nonspecific inhibitor of reactions involving arachidonate, including phospholipase A_2, **prostaglandin-endoperoxide synthase**, and **lipoxygenase**.

eicosatrienoic acid any straight-chain fatty acid having twenty carbon atoms and three double bonds per molecule. The *all-Z*-(5,8,11)-isomer (**Mead acid**) is synthesized in mammals in essential fatty-acid deficiency. The *all-Z*-(8,11,14)-isomer, known also as dihomo-(6,9,12)-linolenic acid (*or* dihomo-γ-linolenic acid), is a precursor of arachidonic acid and of the PG_1 series of **prostaglandins**. The (5,11,14)-isomer has been found in higher plants and algae, cats, marine organisms, and insects.

eicosatriynoic acid any straight-chain fatty acid having twenty carbon atoms and three triple bonds per molecule. 5,8,11-eicosatriynoic acid (*abbr.*: ETI) is an agent that selectively inhibits 5- and 12-**lipoxygenase** without inhibiting **prostaglandin-endoperoxide synthase**.

eicosenoic acid any straight-chain fatty acid having twenty carbon atoms and one double bond per molecule. The 9*E*-isomer is gadelaidic acid (*see* **gadelaidate**); the 9*Z*-isomer is gadoleic acid (*see* **gadoleate**), a constituent of fish oils; and the 11*Z*-isomer is gondoic acid, present in seeds and fish oils.

EID *abbr. for* electroimmunodiffusion.

eIF *abbr. for* eukaryotic initiation factor (*see* **initiation factor**).

Eigen, Manfred (1927–), German physical chemist noted for developing techniques for the study of rapid reactions and applying them to problems of molecular biology; Nobel Laureate in Chemistry (1967), the prize being shared with R. G. W. Norrish and G. Porter 'for their studies of extremely fast chemical reactions, effected by disturbing the equilibrium by means of very short pulses of energy'.

eigenfunction a solution of a differential equation that has solutions only for particular values of some parameters.

eigenvalue any one of the possible values for a parameter of an equation for which the solution will be compatible with the boundary conditions.

Eijkman, Christiaan (1858–1930), Dutch physician, bacteriologist, and nutritionist noted for observing that unpolished rice grains contained an antiberiberi principle (later recognized as a vitamin and named vitamin B_1 or thiamine) and for being the first to produce a dietary deficiency disease experimentally; Nobel Laureate in Physiology or Medicine (1929) 'for his discovery of the antineuritic vitamin' [prized shared with F. G. Hopkins].

einstein a non-SI unit used to express the energy associated with one mole of photons during a photochemical reaction. 1 einstein = $N_A h\nu$, where N_A is the Avogadro constant, h is the Planck constant, and ν is the particular frequency of the electromagnetic radiation effecting the reaction.

Einstein, Albert (1879–1955), German-born Swiss then US patent examiner and mathematical physicist famous above all for his formulation of both the special theory of relativity (in 1903) and the general theory of relativity (in 1916); Nobel Laureate in Physics (1921) 'for his services to Theoretical Physics, and especially for his discovery of the photoelectric effect'.

Einstein–Sutherland relation a relation between the diffusion coefficient at infinite dilution, D_0, and certain molecular parameters. $D_0 = kT/f$, where T is the thermodynamic temperature, k is the Boltzmann constant, and f is the frictional coefficient of the diffusing particle.

EKG *abbr. (US) for* **1** electrocardiograph. **2** electrocardiogram.

elafin *another name for* **SKALP**. [From elastase f inhibitor. The

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'f' was inserted to avoid confusion with elastin and gives an association to the Latin *finire*, to terminate.]

elaidate **1** *numerical symbol*: 18:1(9); *the trivial name for* (*E*)-octadec-9-enoate; CH_3–$[CH_2]_7$–CH=CH–$[CH_2]_7$–COO^- (*trans* isomer); the anion derived from elaidic acid, (*E*)-octadec-9-enoic acid, a monounsaturated straight-chain higher fatty acid. **2** any mixture of free elaidic acid and its anion. **3** any salt or ester of elaidic acid. *Compare* **oleate**.

elaidinization *or* **elaidinisation** the *cis* to *trans* isomerization of mono- and polyunsaturated fatty acids, as in the isomerization of oleic acid to elaidic acid brought about by treatment with nitrous acid or by the action of rumen bacteria.

elaidoyl *the trivial name for* (*E*)-octadec-9-enoyl; CH_3–$[CH_2]_7$–CH=CH–$[CH_2]_7$–CO– (*trans* isomer); the acyl group derived from elaidic acid, (*E*)-octadec-9-enoic acid. It occurs in acylglycerols to an appreciable extent in the body fats of ruminants, possibly having arisen from oleic acid by elaidinization. *Compare* **oleoyl**.

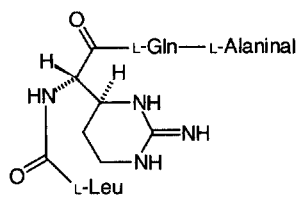
elaioplast any oil-storing **leukoplast** that occurs in plant cells.

ELAM *abbr. for* endothelial leukocyte adhesion molecule; i.e. E-selectin (*see* **selectin**).

elasmobranch **1** any member of the subclass Elasmobranchii, comprising fishes with cartilaginous skeletons such as sharks, skates, and rays. **2** of, pertaining to, or relating to the Elasmobranchii.

elastase historically, any proteinase that hydrolyses elastin. However, the name is now applied to a group of enzymes that vary in specificity. **Pancreatic elastase**, EC 3.4.21.36 (*other names*: pancreatopeptidase E; pancreatic elastase I), catalyses the hydrolysis of proteins, including elastin, with preferential cleavage at Ala-|-Xaa. Example (domestic pig): database code NRL_3EST, 240 amino acids (25.88 kDa); 3-D structure known. **Pancreatic elastase II**, EC 3.4.21.71, preferentially cleaves the carbonyl side of Leu, Met, and Phe. **Leukocyte elastase** EC 3.4.21.37 (*other names*: lysosomal elastase; neutrophil elastase; bone marrow serine protease; medullasin), catalyses the hydrolysis of proteins, including elastin, with preferential cleavage at Val-|-Xaa > Ala-|-Xaa. Pancreatic elastase and leukocyte elastase, in common with most elastases, are serine proteinases, but others, e.g. elastase (EC 3.4.24.26) from *Pseudomonas aeruginosa*, are zinc-containing metalloproteinases. **Elastase III** is pancreatic endopeptidase E (EC 3.4.21.70; *other name*: cholesterol-binding proteinase); it shows preferential cleavage at Ala-|-Xaa, but does not hydrolyse elastin.

elastatinal a peptide produced by actinomycetes that inhibits serine proteineases, particularly elastase.



elastic *(of a body or a substance)* capable of returning to its original shape after deformation. —**elasticity** *n.*

elasticity coefficient *symbol*: ε_S^v; for a metabolic system in a steady state, the fractional change in the velocity, v, of an enzyme step caused by a fractional change in substrate, effector, or product concentration, S. It is given by:

$$\varepsilon_S^v = \frac{S}{v}\left(\frac{\partial v}{\partial S}\right)_{y,z,\ldots} = \frac{\partial \ln v}{\partial \ln S}$$

Since the elasticity coefficient is defined as the partial derivative of a velocity, v, with respect to S (multiplied by the scaling factor, S/v) all other variables that are able to influence the rate through the enzyme are held constant. There are, for any reaction, as many elasticity coefficients as there are metabolites and effectors that interact with the enzyme in question. *See also* **controllability coefficient**, **response coefficient**, **sensitivity coefficient**.

elastin a major structural protein of mammalian connective tissues, especially elastic fibres, and found at sites such as the aorta, nuchal ligament, and lung. Glycine makes up one third of the amino-acid residues in elastin; glycine, proline, alanine, and valine together account for over 80% of its residues. The polymeric chains are cross-linked together into an extensible 3-D network, lysinonorleucine and desmosine cross-links being formed between allysine and lysine residues. A soluble precursor of elastin, **proelastin**, has been isolated from copper-deficient pigs in which the formation of allysine is blocked. Example (precursor) from human: database code ELS_HUMAN, 730 amino acids (63.19 kDa).

elastonectin a protein, M_r 120 000, from human skin fibroblasts and associated with adhesion of mesenchymal cells to elastic fibres.

elective theory of immunity *an alternative name for* **selective theory of immunity**

electrical coupling the phenomenon of ion transport across a membrane, in the absence of a cation–anion cotransport system, when the movement of anions and cations, following the law of electroneutrality, is governed only by the passive permeabilities of the membrane to the ions in question.

electric birefringence a form of **birefringence**, also known as the **Kerr effect**, caused by the alignment of (macro)molecules in an electric field.

electric capacitance *see* **capacitance**.

electric cell an apparatus consisting of two reversible electrodes dipping into the same solution, or into separate solutions electrically connected through an electrolyte bridge. It is used to generate an electromotive force, for electrolysis, or to measure the chemical activity of a chemical species in one of the solutions. *See also* **half-cell**.

electric charge *or* **quantity of electricity** *symbol*: Q *or* q; the attribute of certain elementary particles that is responsible for electric phenomena. Electric charge may be of two kinds, positive or negative, which interact electromagnetically such that like charges repel one another while unlike charges are attracted one to another. The SI derived unit of electric charge is the coulomb. *See also* **charge** (def. 3).

electric conductance *or* **conductance** *symbol*: G; a measure of the readiness with which an electric current can flow through a given component of a circuit. For a direct-current circuit it is equal to the reciprocal of the resistance; for an alternating-current circuit it is equal to the resistance divided by the square of the impedance. The SI derived unit of conductance is the siemens. *See also* **mho**.

electric current *or* **current** *symbol*: I *or* i; one of the seven SI base physical quantities – flow of electric charge through a conductor. The magnitude of a current is given by the amount of charge flowing per unit time. The SI base unit of electric current is the ampere.

electric dichroism the form of **dichroism** (def. 1) caused by orientation of (macro)molecules in an electric field.

electric dipole moment *see* **dipole moment**.

electric double layer *an alternative name for* **electrochemical double layer**.

electric field a **field** in which a stationary electric charge, Q, experiences a force, F, proportional to the magnitude of the charge. The electric field strength, E, is given by: $E = F/Q$; it is expressed in V m^{-1}. If the field is produced by other stationary charges it is called an **electrostatic field**. *Compare* **Coulomb's law**.

electricity **1** any of the forms of energy associated with moving or stationary electrons, protons, or other charge-bearing entities (whether molecular or otherwise). **Static electricity** is associated with stationary charges, **current electricity** with moving charges. **2** the science dealing with electricity.

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electric potential *or* **potential** *symbol*: V *or* ϕ; the work done in bringing unit electric charge from infinity to a specified point in an electric field. The SI derived unit of electric potential is the volt.

electric potential difference *or* **potential difference** *symbol*: E *or* U *or* ΔV *or* $\Delta\phi$; *abbr.*: pd; the work done when a unit electric charge is moved between two points having different electric potentials. If the points are joined by a conductor an electric current will flow between them. The SI derived unit of electric potential difference is the volt. *Compare* **electromotive force**.

electric resistance *or* **resistance** *symbol*: R; the impediment to the flow of an electric current through a component of a circuit, a medium, or a substance. The SI derived unit of resistance is the ohm.

electro+ *or (sometimes before a vowel)* **electr+** *comb. form* indicating electric, electrically, electrolytic.

electroblot *see* **electrophoretic transfer**.

electroblotting *an alternative name for* **electrophoretic transfer**.

electrochemical analysis *or* **electrochemical assay** a chemical analysis or assay performed by means of electrolysis or electrodeposition.

electrochemical double layer any double layer of charges formed in a solution by the adsorption of a layer of ions of opposite charge at the surface of another charge-carrying phase, e.g. the walls of the vessel or the surface of a macromolecule.

electrochemical equivalent the mass of an ion deposited or liberated by the passage of 1 coulomb of electricity. In grams it is 1/96487 of the **chemical equivalent**.

electrochemical potential *symbol*: $\tilde{\mu}$; the change in free energy occurring when a charged solute is transported either up or down a concentration gradient. It is the sum of the free energy changes due both to the concentration gradient and to the electric potential. It is expressed in J mol^{-1}.

electrochemical series *an alternative name for* **electromotive series**.

electrochemistry the branch of science concerned with the study of electrolysis, electrolytic cells, and the applications and properties of ions in solution. —**electrochemical** *adj.*

electrochromatography the form of **chromatography** in which separation of the constituents of a mixture is due to the effect of a constant electric field. *See also* **zone electrophoresis**.

electrochromism any reversible change in optical absorption or emission spectra of a molecule in the condensed phase due to an external electric field. *Compare* **photochromism**, **thermochromism**. —**electrochromic** *adj.*

electrocortin *the former name for* **aldosterone** (before establishment of its structure).

electrocrystallization *or* **electrocrystallisation** **electrodeposition** that results in crystal formation.

electrode any conductor, such as metal, metal covered with one of its salts, carbon, or a thin glass or other membrane, used to establish electric contact with a solution or other nonmetallic part of an electric circuit. The potential assumed by the electrode may depend on the (thermodynamic) activity of one of the solutes in the solution with which it is in contact. *See also* **anode**, **calomel electrode**, **cathode**, **enzyme electrode**, **hydrogen electrode**, **ion-selective electrode**, **oxygen electrode**, **quinhydrone electrode**, **reference electrode**.

electrodecantation *or* **electrophoresis convection** a technique for separating and fractionating proteins and other sols that exploits local differences in concentration and density that may occur during **electrodialysis**. Under the influence of gravity such density differences lead to large-scale separation of sols of high and of low concentrations. This results in a gradual increase in the concentration of a sol in the lower layers of the solution and a decrease in the upper layers.

electrodeposition the deposition of material from a dissolved or suspended state onto an electrode by the application of an electric field; it includes **electrocrystallization**.

electrode potential *symbol*: E; the electric potential between a reversible electrode and the solution in which it is immersed. It may be due to the loss or gain of electrons, if the solution contains a redox couple, or to the formation of ions from unchanged atoms or of atoms from ions, if the solution contains ions of a chemical element present as uncharged atoms in the electrode.

electrodialysis a form of **dialysis** conducted in the presence of an electric field across the membrane(s). It is useful for quickly removing ionic microsolutes from a solution containing nondiffusible material.

electroelution a technique in which application of an electric potential causes biomolecules to be transferred from an electrophoresis gel to a membrane during **blotting** procedures. *See also* **transfer membrane**.

electroendosmosis *a former term for* **electroosmosis**. —**electroendosmotic** *adj.*

electrofocusing *a newer name for* **isoelectric focusing**.

electrofuge *(in chemistry)* a leaving group in a reaction that does not carry away the bonding electron pair.

electrogenesis the generation of an electrochemical potential gradient, esp. across a membrane.

electrogenic pump any biological system that generates an electrochemical potential across a membrane by pumping one ion across the membrane without the concomitant movement of another ion of the same charge in the opposite direction.

electroimmunoassay *the original name for* **rocket immunoelectrophoresis**.

electroimmunodiffusion *abbr.*: EID; any technique for the analysis of antigenic macromolecules in which a combination of electrophoresis and immunodiffusion is employed. Four types may be distinguished: (1) one-dimensional single, i.e. **rocket immunoelectrophoresis**; (2) one-dimensional double, i.e. **counter immunoelectrophoresis**; (3) two-dimensional single, i.e. **crossed immunoelectrophoresis**; and (4) two-dimensional double, not so far individually named or much used.

electroimmunodiffusogram the immunoprecipitation pattern produced by any type of **electroimmunodiffusion**.

electrokinetic potential *or* **zeta potential** *symbol*: ζ; the potential drop across the mobile part of an **electrochemical double layer** that is responsible for electrokinetic phenomena. The electrokinetic potential is positive if the potential increases from the bulk of the liquid phase towards the interface.

electrolectin a lectin of the **galaptin** family from *Electrophorus electricus*, and the name of a group of β-D-galactoside-binding lectins found in teleosts, amphibians, and mammals. Example from *E. electricus*: database code LEG_ELEEL, 129 amino acids (14.44 kDa).

electrolysis the chemical change produced by passing a direct electric current through a solution of an electrolyte, or through a fused electrolyte. Positively charged ions (cations) move towards the cathode and negatively charged ions (anions) move towards the anode, thus carrying the electric current. At the electrodes the positively charged ions gain electrons and negatively charged ions give up electrons, forming uncharged atoms, molecules, or radicals, which may either be deposited on the electrode or react with the electrode, the solvent, or each other. Alternatively, atoms of the electrode material may ionize and go into solution.

electrolyte any substance that, when in solution or molten, can undergo (partial or complete) dissociation into ions and hence is able to conduct an electric current by the movement of the ions.

electrolyte balance *(in physiology)* the sum total of the reactions and processes concerned with the maintenance of a constant internal environment in the body with respect to the distribution of ions between the various fluid compartments and excretions.

electrolytic **1** of, pertaining to, or produced by **electrolysis**. **2** of or pertaining to an **electrolyte**.

electrolytic conductivity *or (formerly)* **specific conductance** *symbol*: κ; the ability of an electrolyte to permit the flow of

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electric current, defined by the equation: $\kappa = j/E$, where j is the electric current density and E is the electric field strength. In SI units, κ is in S m $^{-1}$, j in A m^{-2}, and E in V m^{-1}. Electrolytic conductivity is usually measured in a rigid conductivity cell whose cell constant has been determined by means of a reference potassium chloride solution.

electromagnetic **1** of, relating to, or involving both electricity and magnetism; having both electrical and magnetic properties. **2** of or relating to **electromagnetic radiation**. **3** **a** of, relating to, containing, or operated by an electromagnet. **b** of or relating to electromagnetism.

electromagnetic radiation *abbr.*: emr *or* EMR; radiation consisting of transverse waves of energy with associated electric and magnetic fields that can be represented by vectors at right angles to each other and to the direction of its propagation. The radiation results from the acceleration of electric charges and can be propagated through free space (i.e. it requires no supporting medium). The characteristics of the radiation vary with the frequency (or the wavelength) of the wave motion, the range of possible frequencies constituting the **electromagnetic spectrum**. From the low-frequency end of the spectrum to the high end are ranged: **radiofrequency radiation**, **infrared radiation**, visible radiation or **light**, **ultraviolet radiation**, **X-rays**, and **gamma-radiation**. Radiation of all frequencies travels at the same velocity through space. The speed of light in vacuum, c_0, is defined as 299 792 458 m s $^{-1}$.

electromagnetic unit *abbr.*: emu *or* EMU; any of the electrical units based on the magnetic properties of electric currents. The force, F, between two magnetic poles of strength m_1 and m_2 placed a distance d apart in a medium of permeability μ is given by $F = m_1m_2/\mu d^2$. If F, μ, and d each be unity and if $m_1 = m_2 = m$, then m_1 and m_2 are poles of unit strength. Units based on this definition of m are electromagnetic units and are denoted by the prefix 'ab+'.

electromeric effect an obsolescent term for a molecular polarizability effect occurring by intramolecular electron displacement characterized by the substitution of one electron pair for another in the same atomic octet of electrons.

electrometer any instrument of very high input impedance that is used for detecting or measuring (changes in) the magnitude of an electric potential difference or electric charge esp. if of small value. Hence it is useful also for the (indirect) measurement of a very low electric current or a very high electric resistance, and for the detection or measurement of ionizing radiation. —**electrometric** *adj.*

electrometric titration **1** *an alternative name for* **potentiometric titration**. **2** *a name sometimes used generically for* **conductometric titration** and **potentiometric titration**.

electromotive force *abbr.*: emf *or* EMF; *symbol*: E; the energy supplied by a source of electric current in driving unit electric charge through an electric circuit. The SI derived unit of electromotive force is the volt. *Compare* **electric potential difference**.

electromotive series *or* **electrochemical series** a series in which the metals are arranged in decreasing order of their tendency to form cations by a reaction of the type: $M \rightleftharpoons M^+ + e^-$.

electromyogram *abbr.*: EMG; the tracing produced by an **electromyograph**.

electromyograph an instrument for detecting and recording the electrical activity of a muscle or group of muscles.

electron **1** *symbol*: e *or* e^- *or* β^-; a negatively charged elementary particle of rest mass, m_e, $\approx 9.109\ 39 \times 10^{-31}$ kg and electric charge $1.602\ 177\ 33(49) \times 10^{-19}$ C. It is sometimes termed a **negatron**, especially to distinguish it from its antiparticle, the positron. Electrons are present orbiting in all atomic nuclei and are involved in the formation of bonds between atoms. Specific designations of electrons in atoms and molecules include: **σ-electrons**, which participate in single bonds; **π-electrons**, which participate in double or triple bonds; and **p-electrons**, which participate in unshared electron pairs. **2** *(sometimes)* either a negatron (i.e. **electron** (def. 1)) or a **positron**. *See also* **beta-particle**.

electron acceptor **1** any substance to which an electron may be transferred. **2** *an alternative name for* **Lewis acid** (use discouraged). *Compare* **electron donor**.

electron affinity **1** the degree to which any molecular entity attracts one or more additional electrons. **2** *symbol*: E_{ea}; the minimum energy, expressed in joules, needed to remove an electron from a negatively charged molecular entity, or the reciprocal of the energy required to introduce an electron into a molecular entity.

electron-affinity spectroscopy a sensitive ionization method for the qualitative analysis of small quantities of organic compounds separated by gas chromatography, based on the differences in electron-capture ability that exist between the principal classes of organic compounds. The substances to be detected are passed through an ionized gas; the detector is sensitive to the resulting reduction in current.

electron capture **1** *or* **K-capture** *abbr.*: EC; a mode of decay of radionuclides in which an electron from an inner orbit of a decaying atom is absorbed into its nucleus, wherein a proton is converted to a neutron. Rearrangement of the orbital electrons then leads to the emission of characteristic X-radiation (*see* **X-radiation**). Generally the captured electron is derived from the K-shell, hence the alternative name. **2** *see* **electron-affinity spectroscopy**.

electron-capture detector *abbr.*: ECD; the type of detector used in **electron-affinity spectroscopy**.

electron carrier any molecular entity that serves as an electron acceptor and electron donor in an electron transport system.

electron-dense describing any structure, material, or compound that scatters an impinging electron beam, thus becoming apparent in **electron microscopy**, etc.

electron-dense label any atom group or substance (e.g. ferritin) that is **electron-dense** and that has been or may be attached in a specific manner to compounds or structures so as to show them up by electron microscopy, etc.

electron density the electron probability distribution in any molecular entity. If $P(x,y,z)$ is the electron density at the point with coordinates x,y,z, then the probability of finding an electron in the volume element $dxdydz$ is $P(x,y,z)\ dxdydz$. In, e.g., X-ray scattering experiments the scattering at this position is proportional to this probability. The term is often wrongly applied to negative **charge density**.

electron-density map a three-dimensional representation of the structure of a molecule or substance derived from X-ray diffraction data and made by the superposition of the electron-density contours of a series of imaginary parallel planes through the specimen being examined.

electron diffraction an effect observed when a narrow beam of electrons passes through a layer of material, e.g. a crystal, and is deflected by this material. The effect is due to the wave-like nature of electrons.

electron donor **1** any substance that is able to transfer an electron to another chemical species. **2** *an alternative name for* **Lewis base** (use discouraged). *Compare* **electron acceptor**. *See also* **donor atom**.

electron donor–acceptor chromatography *see* **charge-transfer chromatography**.

electron donor–acceptor complex *(sometimes) an alternative name for* **1** **charge-transfer complex** (use not recommended). **2** **Lewis adduct** (use not recommended).

electronegative **1** describing an atom or a group of atoms that tends to attract electrons, especially in the formation of a covalent bond. **2** describing any chemical or other entity that carries a negative charge and hence tends to move to the anode in electrophoresis.

electronegativity a measure of the power of an atom or group of atoms to attract electrons to itself from other parts of the same molecular entity.

electron equivalent the **equivalent** of any oxidizing (or reducing) agent that is equivalent to one entity of electrons.

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electroneutrality condition the condition that in any solution the sum of the negative electric charges on ions must be equal to the sum of the positive charges on ions.

electron-exchange resin any synthetic resin containing groups able to undergo reversible oxidation–reduction reactions; such resins are useful as insoluble oxidizing or reducing agents.

electron gun a device used in electron microscopes, mass spectrometers, and other instruments to generate a beam of high-velocity electrons. It consists of a white-hot tungsten filament, as the electron source, and an anode kept at a potential of several tens of kilovolts above that of the filament. The electrons are accelerated towards the anode, which contains a small orifice through which some of the fastest electrons pass to form the electron beam.

electron hole the hole in the valency structure of an atom created by the absence of an electron when the energy level of an electron is raised from the valency band to the conduction band. The hole has a great tendency to recapture an electron. *See also* **hole**.

electronic **1** of or relating to an electron or electrons. **2** of, relating to, or operated by **electronics** (def. 2).

electronics **1** *(functioning as sing.)* the branch of science and technology concerned with electronic devices and circuits and with their development and applications. **2** *(functioning as pl.)* the circuits, devices, and equipment that function by the passage of electrons through semiconductors, transistors, and thermionic valves.

electronic transition the passage of an electron in a chemical entity from one energy level to another.

electron lens any arrangement of coils and/or electrodes producing a magnetic and/or an electric field used to focus an electron beam, e.g. in an electron microscope.

electron micrograph any photograph of an object taken with an **electron microscope**.

electron microscope *abbr.*: EM *or* e.m.; an instrument in which a magnified image of a sample is produced using a beam of high-energy electrons. The electrons are accelerated by means of an **electron gun**, using voltages in the range 40–100 kV, and the apparatus is evacuated to minimize electron scatter by air. In the **transmission electron microscope** (*abbr.*: TEM) the electron beam is focused onto a thin sample by a combination of magnetic and electric lenses and, after passing through the sample, the electrons are focused onto a fluorescent screen or photographic plate. The resolving power can be as great as 0.2–0.5 nm. In **cryoelectron microscopy**, lightly fixed frozen sections are employed. If these are used for the detection of antigens with antibodies coupled to colloidal gold, the technique is called **cryoimmunoelectron microscopy**. In the **scanning electron microscope** (*abbr.*: SEM) a narrow beam of electrons is made to scan to and fro across the sample by a varying field, and emitted **secondary electrons** are focused onto a screen to produce an image of the specimen. The specimen may be thicker than in the transmission electron microscope and, though resolution is lower with the scanning instrument, the depth of field is greater and the image gives a three-dimensional effect.

electron multiplier an electronic device for detecting, and counting, electrons, using **secondary emission**. It consists of an evacuated tube containing a series of electrodes, each held at a higher positive electric potential than the preceding one. When an electron hits the first electrode two or more **secondary electrons** are emitted; these are accelerated to the second electrode, where more electrons are produced, and so on.

electron nuclear double resonance *abbr.*: ENDOR; a phenomenon in nuclear magnetic resonance spectroscopy in which saturation of an electron resonance by the simultaneous application of a microwave field causes, under appropriate conditions, an improvement of the resolution of nuclear hyperfine structures.

electron optics the branch of science concerned with the effects of electric and magnetic fields on the movement of electrons, especially with the focusing and deflection of electron beams in **cathode-ray tubes**, **electron microscopes**, and similar devices.

electron paramagnetic resonance spectroscopy *an alternative name for* **electron spin resonance spectroscopy**.

electron probe X-ray microanalysis a highly sensitive technique for elemental microanalysis based on the frequencies and/or intensities of the characteristic X-rays emitted by each element present in a sample when it is excited by a beam of accelerated electrons.

electron sink *or* **electron trap** an **electrophilic** atom or group of atoms that can capture an electron from another part of a molecular system.

electron spectroscopy for chemical analysis *abbr.*: ESCA; *see* **photoelectron spectroscopy**.

electron spin *see* **spin** (def. 3).

electron spin-echo spectroscopy a technique giving precise values for electron spin relaxation times, in which intense microwave pulses at a frequency satisfying the resonance condition are applied to a paramagnetic sample in a magnetic field. Phase coherence in the spins is lost through relaxation when the pulse is switched off but can be restored by a second pulse 180° out of phase. The restoration of phase coherence gives rise to a nuclear induction signal (the echo).

electron spin-lattice relaxation time *(in* **electron spin resonance spectroscopy***)* a measure of the time taken for the spin population to return to its equilibrium value by interaction with the fluctuating internal electric fields surrounding it.

electron spin resonance spectroscopy *abbr.*: ESR (spectroscopy); a technique, also called **electron paramagnetic resonance spectroscopy** (*abbr.*: EPR (spectroscopy)) and analogous to **nuclear magnetic resonance spectroscopy**, that is used to investigate paramagnetic centres in the system under study; only electrons whose spin is not paired with the oppositely directed spin of another electron give an ESR signal. Useful information is obtained by this technique about certain transition-metal ions (notably Cu^{2+}), (free) radicals, and free electron centres such as may be produced by X-irradiation of (macro) molecules. A **probe** (def. 2) giving an ESR signal may be incorporated into membrane lipids or attached to proteins to enable otherwise inaccessible systems to be studied by this technique.

electron spin–spin relaxation time *(in* **electron spin resonance spectroscopy***)* a measure of the time taken for phase coherence to be lost and equilibrium to be re-established through interaction with neighbouring spins. It is inversely proportional to the line width of the signal.

electron-transfer flavoprotein *or* **electron-transferring flavoprotein** *abbr.*: ETF; a protein containing flavin adenine dinucleotide (FAD) that together with an acyl-CoA dehydrogenase (EC 1.3.99.3) forms a system that oxidizes an acyl-CoA molecule and reduces ubiquinone and other acceptors in the mitochondrial electron transport system.

electron-transferring flavoprotein dehydrogenase *abbr.*: ETF dehydrogenase EC 1.5.5.1; an enzyme that catalyses the oxidation of reduced ETF by ubiquinone to form ETF and ubiquinol. The ubiquinol is then oxidized by **ubiquinol–cytochrome *c* reductase**. It is an iron–sulfur flavoprotein involved in coupling the **beta-oxidation system** to the **respiratory chain**. *See also* **electron-transferring flavoprotein**.

electron-transferring fluoroprotein *see* **azurin**.

electron transport **1** **respiratory electron transport**; the process by which pairs of electrons derived from intermediates of the **tricarboxylic-acid cycle** and other substrates flow down the **respiratory chain** to dioxygen, the ultimate electron acceptor in respiration. **2** **photosynthetic electron transport**; the process by which pairs of electrons are transported from H_2O to $NADP^+$ in the light phase of photosynthesis during noncyclic **photophosphorylation**.

electron-transport chain *an alternative name for* **respiratory chain**.

electron trap *an alternative name for* **electron sink**.

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electronvolt *or* **electron volt** *symbol*: eV; a non-SI unit of energy equal to the kinetic energy acquired by an electron when accelerated through an electric potential difference of 1 volt. 1 eV = $e \times V \approx 1.602\ 18 \times 10^{-19}$ J, where e is the **elementary charge** and V is the volt.

electroosmosis *or (formerly)* **electroendosmosis** the motion of a liquid through a membrane (or plug or capillary) consequent upon the application of an electric field across the membrane. A similar phenomenon may occur in electrophoresis, where many of the supporting media used, e.g. paper or agar, acquire negative charges during electrophoresis at alkaline pHs and, since the medium cannot move, H_3O^+ ions move towards the cathode, giving the effect of an osmotic movement of solvent towards the cathode and making electrically neutral molecules appear to be cationic. —**electroosmotic** *adj.*

electropherogram *a variant spelling of* **electrophoretogram**.

electrophile *or* **electrophilic reagent** any chemical species that is preferentially attracted to a region of high electron density in another species during a chemical reaction. Such reagents normally are positively charged or contain electron-deficient chemical groups. They tend to react with electron-rich or negatively charged chemical species. *Compare* **nucleophile**.

electrophilic **1** of, pertaining to, or being an **electrophile**; having or involving an affinity for regions of high electron density in a chemical reactant. **2** describing a chemical reaction in which an electrophile participates.

electrophilic catalysis catalysis by a Lewis acid, i.e. any chemical species that abstracts an electron pair from the reactant.

electrophilic displacement *an alternative term for* **electrophilic substitution reaction**.

electrophilicity the relative reactivity of an **electrophile**, measured by the relative rate constants of different electrophiles towards a common reactant.

electrophilic reagent *an alternative name for* **electrophile**.

electrophilic substitution reaction *or* **electrophilic displacement** a chemical reaction in which an **electrophile** effects heterolytic substitution in another reactant, both bonding electrons being supplied by that other reactant.

electrophoresis **1** the phenomenon of the movement of ions (including macromolecular ions) or charged particles or ions through a fluid under the influence of an electric field applied to the fluid. A number of different media have been used as the fluid support, including paper, cellulose acetate, starch gel, and polycrylamide gel. Ions or particles bearing a net positive charge tend to move towards the negative pole of the electric field and vice versa, the rate of movement of a particular variety of ion or particle depending, *inter alia*, on its charge-to-mass ratio. The phenomenon has been widely applied in separating proteins, nucleic acids, and other charged molecular species for analytical or preparative purposes, and also in the analytical or preparative fractionation of heterogeneous populations of dispersed cells or other types of macroscopic particles. **2** the act or process of causing ions or charged particles so to migrate; any technique based upon such a phenomenon, e.g. **continuous flow electrophoresis**, **immunoelectrophoresis**, **moving boundary electrophoresis**, **paper electrophoresis**, **polycrylamide gel electrophoresis**, **zone electrophoresis**. *See also* **electrodecantation**. —**electrophoretic** *adj.*

electrophoresis convection *an alternative term for* **electrodecantation**.

electrophoretic effect the phenomenon of decreased **electrophoretic mobility** of a charged macromolecule caused by the movement of counter ions and/or solvent molecules in the opposite direction to that of the macromolecule.

electrophoretic mobility *symbol*: u; the **electrophoretic velocity**, v, of a charged particle expressed per unit field strength; hence, $u = v/E$, where E is the field strength. The value of u is positive if the particle moves towards the pole of lower potential and negative in the opposite case. The electrophoretic mobility depends only on molecular parameters.

electrophoretic molecular sieving *(sometimes) an alternative term for* **polyacrylamide (gel) electrophoresis**.

electrophoretic titration curve the pH-mobility curve of an ampholyte, e.g. a protein, generated by subjecting a zone of it to electrophoresis in a gel slab at right angles to a preformed, stationary pH gradient. *Compare* **isoelectric focusing**.

electrophoretic transfer *or* **electroblotting** a development of the technique of blot transfer, in which proteins or nucleic acids are transferred from a separation gel to nitrocellulose or diethylaminoethyl- (DEAE-)cellulose membranes or to diazobenzyloxymethyl- (DBM)- or diazophenylthioether- (DPT-) paper by electrophoresis, rather than by capillary flow, with a consequent decrease in the time required for the transfer. The membrane or paper bearing a resultant pattern of separated substances has been termed an **electroblot**. *See* **blotting**.

electrophoretic velocity *symbol*: v; the velocity of a charged particle during electrophoresis. It is normally proportional to the electric field strength. *Compare* **electrophoretic mobility**.

electrophoretogram *or* **electropherogram** the result of a zone-electrophoretic separation, either directly visible or after staining or processing to produce a graph.

electrophysiology the part of physiology concerned with the electrical phenomena associated with bodily processes, such as nervous and muscular activity.

electroporate to create momentary pores in the membranes of living cells, without loss of their viability, by exposing them to a sequence of brief electrical pulses of high field strength. The reversible breakdown of the cell membranes thus caused enables treated cells to take up exogenous material (e.g. drugs or foreign DNA). —**electroporated** *adj.*; **electroporation** *n.*

electroporator an apparatus or device for effecting electroporation.

electropositive **1** describing an atom or group of atoms that tends to give up electrons, especially in the formation of a covalent bond. **2** describing any chemical or other entity that carries a positive charge and hence tends to move to the cathode in **electrophoresis**.

electropositivity a measure of the power of an atom or group of atoms to give up electrons to other parts of the same molecular entity.

electrospray a technique used in **mass spectrometry** in which a dilute acidic solution of the macromolecule is sprayed from a metal syringe needle maintained at +5000 V, forming fine highly charged droplets from which the solvent rapidly evaporates.

electrostatic of or pertaining to static electricity or electrostatics.

electrostatic bond any valency linkage between atoms arising from the transfer of one or more outer-shell electrons of one atom to the outer shell of another atom, leading to more complete outer shells in both atoms. The dissociation of an electrostatic bond leads to the production of ions.

electrostatic field any **electric field** produced by stationary charges.

electrostatic interaction any of the attractive or repulsive forces between atoms and/or groups of atoms and/or molecules that are due to the presence of ionized chemical entities and to the electronegative and electropositive properties of these atoms, groups, or molecules. *Compare* **electric field**.

electrostatic precipitation the removal of small particles suspended in a gas by electrostatic charging followed by precipitation onto a highly charged collector.

electrostatics the branch of physics concerned with static electricity.

electrostatic units *abbr*: esu *or* ESU; a system of electrical units, used in the cgs system, based upon the electrostatic unit of electric charge, i.e. the quantity of electricity that will repel an equal quantity of electricity, 1 cm distant from it in a vacuum, with the force of 1 dyne.

electrostriction the reversible change in dimensions of a dielectric when an electric field is applied to it. For example, the

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electrostatic field associated with a dissolved electrolyte causes a shrinkage in the volume occupied by the solvent.

electrotaxis the directional movement of an organism in an electric field. —**electrotactic** *adj.*

electrotropism any orientation response of a sessile organism to an electrical stimulus.

electrovalency *or (esp. US)* **electrovalence** **1** the type of **valency** characterized by the transfer of one or more electrons from one atom to another atom, with the formation of ions. **2** the number of negative or positive charges acquired by an atom by the respective gain or loss of electrons. —**electrovalent** *adj.*; **electrovalently** *adv.*

electrovalent bond *an alternative term for* **ionic bond**.

electroviscosity the, usually minor, change in viscosity that occurs when an electric field is applied to some polar liquids.

eledoisin a **tachykinin** with the structure Glp-Pro-Ser-Lys-Asp-Ala-Phe-Ile-Gly-Leu-Met-NH_2; it is obtained from the posterior salivary glands of small octopus (*Eledone* spp.). It is more potent than **physalaemin** and **substance P** in some assay systems. It is useful as a lachrymal and salivary secretagogue and in the study of receptors for substance P.

element any basic and distinct component of matter that is not resolvable into simpler components with differing chemical properties. Each consists exclusively of atoms with the same unique **proton number** (although such atoms may not necessarily have the same **nucleon number** or **relative atomic mass**). Ninety-three chemical elements are known to occur naturally, either in the free state or in combination with others; to date, a further 16 have been produced artificially. —**elemental** *or* **elementary** *adj.*

elementary analysis any quantitative chemical analysis of the amounts of different chemical elements present in a sample.

elementary charge *or* **proton charge** *symbol*: e; a fundamental physical constant representing the electric charge on one electron (or proton). Its recommended value is $1.602\ 177\ 33\ (49) \times 10^{-19}$ C.

elementary particle **1** *or* **fundamental particle** any of the particles that form the base units of which all matter is composed. The stable elementary particles are protons, electrons, and neutrinos; they combine with neutrons to form stable atoms. Other, short-lived elementary particles are known. **2** *or* **Fernández-Morán particle** *or* **oxysome** *or* **stalked particle** any of the knoblike structures, 8–9 nm in diameter, seen in the electron microscope on the inner surface of the inner membrane of unfixed mitochondria negatively stained with phosphotungstate.

elementary rest mass *symbol*: m_e; the mass of an electron, it is a fundamental atomic constant, $9.109\ 389\ 7(54) \times 10^{-31}$ kg.

eleostearate **1** *numerical symbol*: 18:3(9,11,13); *the trivial name for* octadeca-9,11,13-trienoate; CH_3–$[CH_2]_3$–$[CH{=}CH]_3$–$[CH_2]_7$–COO^-; the anion derived from eleostearic acid, octadeca-9,11,13-trienoic acid, a triunsaturated straight-chain higher fatty acid. It is a constitutional isomer of (6,9,12)-linolenate with conjugated double bonds. **2** any mixture of free eleostearic acid and its anion. **3** any salt or ester of eleostearic acid. *See also* **eleostearoyl**.

eleostearoyl *symbol*: eSte; *the trivial name for* octadeca-9,11,13-trienoyl; CH_3–$[CH_2]_3$–$[CH{=}CH]_3$–$[CH_2]_7$–CO–; the acyl group derived from eleostearic acid. The 9*Z*,11*E*,13*E*-isomer occurs naturally as acylglycerols in some seed oils, especially tung oil.

ELF1 a gene encoding transcription factors, related to the protooncogene ***ETS*** and named from E74-like factor (*see* **E74**), a *Drosophilia* protein that binds a regulatory element of the dopa decarboxylase gene. Example from *Drosophila melanogaster*: database code ELF1_DROME, 1063 amino acids (116.15 kDa).

elimination reaction a chemical reaction in which two groups are removed from a molecule of an organic compound without being replaced by other groups. In most such reactions the groups are lost from adjacent carbon atoms: one of the groups eliminated is commonly a hydron and the other a nucleophile, and the elimination results in the formation of a multiple bond. The reverse process is an **addition reaction**.

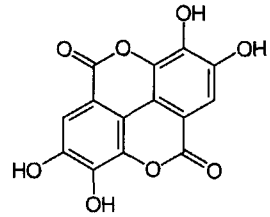
Elion, Gertrude Belle (1918–99), US chemist, biochemist, and pharmacologist distinguished for her introduction, largely in collaboration with her colleague G. H. Hitchings, of a range of widely used synthetic drugs designed as antimetabolites, including the antifolate bactericidal agent **co-trimoxazole**, the immunosuppressants **mercaptopurine** and its derivative **azathioprine**, and the antiviral compound **acycloguanosine**; Nobel Laureate in Physiology or Medicine (1988) jointly with J. W. Black and G. H. Hitchings 'for their discoveries of important principles for drug treatment'.

ELISA *abbr. for* enzyme-linked immunosorbent assay.

Elk a family of cell-surface proteins similar to those encoded by the protooncogene ***ETS*** and with presumed similar function (named from Eph-like kinase); they are protein tyrosine kinases, restricted to brain and testis, having a single transmembrane domain and two fibronectin-like domains. Example from rat (precursor): database code KELK_RAT, 984 amino acids (109.88 kDa).

Elk-1 a gene-regulating protein, found in lung and testis, that binds to DNA at purine-rich sites. It is a substrate for a **MAP kinase** in the phosphorylation cascade originating with activated protein kinase C or Ras; on phosphorylation it forms with the transcription factor **SRF** a ternary complex, which binds to the **serum response element** of DNA, turning on *FOS* transcription. Example (human): database code ELK1_HUMAN, 428 amino acids (44.86 kDa).

ellagic acid 4,4′,5,5′,6,6′-hexahydroxydiphenic acid 2,6,2′,6′-dilactone; a commonly occurring plant polyphenol that inhibits glutathione S-transferase.



ellipse any closed plane figure whose perimeter is the locus of a point that moves so that the sum of its distances from two fixed points, the foci, is constant. An ellipse has two axes of symmetry, the major axis at the furthest distance between opposing points on its circumference and the minor axis at the nearest distance.

ellipsoid any surface or solid figure whose plane sections are all either ellipses or circles. —**ellipsoidal** *adj.*

ellipsoid of rotation *or* **ellipsoid of revolution** a solid figure generated by the rotation of an ellipse about one of its axes. If the rotation is about the major axis the ellipsoid of revolution is said to be **prolate**, whereas if the rotation is about the minor axis it is said to be **oblate**. *See also* **equivalent ellipsoid of rotation**, **spheroid** (def. 2).

ellipsosome a compartment in the retinal cones of fish that contains cytochrome-like pigment.

elliptical of, relating to, or having the shape of an **ellipse** or **ellipsoid**. —**elliptically** *adv.*

elliptically polarized *or* **elliptically polarised** describing light (or other electromagnetic radiation), whose electric vector appears to follow an elliptical path when viewed along the light beam. *See also* **polarized light**.

ellipticity **1** the ratio of the lengths of the major to the minor axis of an **ellipse** or **ellipsoid**. **2** the arc tangent of the ratio of the lengths of the minor to the major axis of an ellipse. *See also* **circular dichroism**, **Cotton effect**, **molecular ellipticity**.

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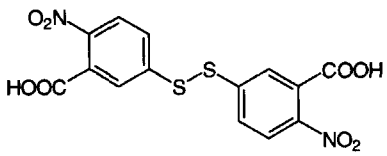
Ellman's reagent 5,5′-dithiobis(2-nitrobenzoic acid) (*abbr.*: DTNB); a reagent used for labelling thiol (SH) groups in protein side-chains. The reagent reacts quantitatively with thiol groups, forming mixed disulfides and releasing the anion 5-sulfido-2-nitrobenzoic acid; this absorbs light at 412 nm, thus permitting the determination of the number of thiol groups in the protein sample. [After George Leon Ellman (1923–).]



elongase any of the long-chain fatty-acyl-coenzyme A elongating enzymes, found in mammalian microsomes, that act on saturated and unsaturated fatty-acyl derivatives having 16 or more carbon atoms per molecule of fatty acid.

elongation factor *abbr.*: EF; any of a group of soluble proteins required for chain elongation during polypeptide synthesis at the ribosome. In *Escherichia coli* there are three elongation factors: EF-Tu, EF-Ts (*see* **EF-T**), and **EF-G**. EF-Tu helps to bind aminoacyl-tRNA, via a tertiary complex, aminoacyl-tRNA·EF-Tu·GTP, to the ribosomal A-site. After EF-Tu-dependent GTP hydrolysis, the EF-Tu·GDP complex dissociates from the ribosome and is recycled to EF-Tu·GTP, probably via an EF-Tu·EF-Ts intermediate. *E. coli* EF-Tu and GTP form ternary complexes with all aminoacyl-tRNAs except the initiator, $tRNA_f^{Met}$EF-G catalyses the GTP-dependent movement of the ribosome and the codon–anticodon-linked mRNA·peptidyl-tRNA complex relative to each other, resulting in the removal of a deacylated tRNA and the location of peptidyl-tRNA from the ribosomal A-site to the P-site. In eukaryotes three proteins, EF-1α, EF-1β, and EF-2, are required for the elongation events. EF-1α, which occurs in different tissues as aggregates of varying size of a polypeptide chain of M_r 53 000, functions during chain elongation, like EF-Tu, to bring the aminoacyl-tRNA to the ribosomal A-site in a reaction in which GTP is hydrolysed. EF-1β, of M_r 30 000, functions as EF-Ts. EF-2, like EF-G, catalyses the translocation of the peptidyl-tRNA from the ribosomal A-site to the P-site in a GTP-dependent reaction. Rat liver EF-2 has an M_r of 110 000, while wheatgerm EF-2 has an M_r of 70 000. *Compare* **initiation factor**, **release factor**.

Elson–Morgan reaction a colorimetric reaction for the estimation of combined and free hexosamines. The specimen is heated in alkaline solution with acetylacetone to form a pyrrole derivative, which then gives a red colour with *p*-dimethylaminobenzaldehyde on acidification. [After Leslie Alderman Elson and Walter Thomas James Morgan (1900–), British biochemist, who together described the reaction in 1933.]

eluant *a variant spelling of* **eluent**.

eluate **1** *(in chromatography)* the solution flowing from a chromatographic column; the desired material in such a solution. **2** *(in immunology)* a solution of material derived from an insoluble or particulate antigen–antibody complex, e.g. by heating or by treatment with an appropriate buffer solution.

eluent *or* **eluant**, a liquid used in **elution**, particularly in **chromatography**.

eluent strength function *(in chromatography)* the order of an **eluotropic series** defined as the adsorption energy per unit area of standard activity of the solvent:

$$\log K = \log V_a + \alpha(S^\circ - A_s\varepsilon^\circ),$$

where K is the distribution coefficient in mass/volume of adsorbent and is independent of the solute concentration, V_a is the adsorbent surface volume, α is an adsorbent function proportional to the average surface energy of the adsorbent, S° is a solute parameter equivalent to the adsorption energy of the solute from solution, A_s the area of absorbant occupied by solvent, and ε° is a solvent strength parameter; the larger ε°, the stronger the solvent.

eluotropic series a series of solvents arranged in the order of their relative abilities to effect **elution**.

elute to wash out or extract retained material, particularly from a chromatography column.

eluting **1** of or relating to **elution**, e.g. an eluting solvent. **2** the process of carrying out an **elution**.

elution the process of washing out or extracting adsorbed material from a chromatographic column.

elution volume *(in chromatography)* the volume of mobile phase that must pass through a chromatographic column, after sample application, to produce a peak in the concentration of a particular solute in the effluent or eluate.

elutriation the process of separating and purifying particles in a powder or suspension according to their rates of sedimentation. It may be effected by repeatedly washing, decanting, and settling, or by allowing a liquid or gas containing the particles to flow upwards (against gravity), when particles whose sedimentation rates are less than the rate of upward flow are washed away from the larger, heavier particles. *Compare* **centrifugal elutriation**, **electrodecantation**.

elutriator a device for grading finely divided material according to the sizes and weights of the particles by means of a stream of liquid or gas.

elymoclavine an **ergot alkaloid** produced by *Claviceps purpurea* and other fungi.

em+ *prefix; a variant of* **en+** *(sometimes before b, m, and p)*.

EM *or* **e.m.** *abbr. for* electron microscope (*or* electron microscopy).

Embden–Meyerhof pathway *or* **Embden–Meyerhof–Parnas pathway** *alternative names for* **glycolytic pathway**. [After Gustav Embden (1874–1933) and Otto **Meyerhof** (1884–1951), German biochemists, and Jacob Karol Parnas (1884–1949), Polish biochemist.]

EMBL *abbr. for* European Molecular Biology Laboratory; an international research facility based at Heidelberg in Germany. The initials are also used as the name of a major database of nucleic acid and protein sequences maintained by EMBL.

EMBO *abbr. for* European Molecular Biology Organization.

embolus (*pl.* **emboli**) a thrombus fragment that is transported in the circulation to distant tissues, where it can cause ischemic tissue damage.

embryo the structure that develops from a **zygote**, up to the time of birth or hatching in eutherian animals, or of germination in plants. In mammals the term is restricted to the structure present in the early part of gestation that develops into a **fetus**. —**embryonic** *adj.*

embryogenesis *or* **embryogeny** the formation of an embryo from an ovum and the processes of its development. —**embryogenic** *adj.*

embryology the branch of biology concerned with the study of embryos and their development. —**embryological** *or* **embryologic** *adj.*; **embryologically** *adv.*; **embryologist** *n.*

embryonated differentiated into, or having an embryo, e.g. an embryonated hen's egg.

embryonic stem cell *abbr.*: ES cell; a **totipotent** cell that can be cultured from an early embryo.

embryonin *another name for* bovine **α_2-macroglobulin**.

emerimicin *see* **peptaibophols**.

Emerson enhancement the phenomenon in photosynthesis in which the **quantum yield** of light in the far-red region of the spectrum is enhanced by weak background illumination with shorter wavelength light. *Compare* **enhancement spectrum**. [After Robert Emerson (1903–59).]

emetic **1** having the power to cause vomiting. **2** any compound with emetic properties.

emetine 6′,7′,10,11-tetramethoxyemetan; an alkaloid from *Cephaelis ipecacuanha* that is a gastrointestinal irritant and

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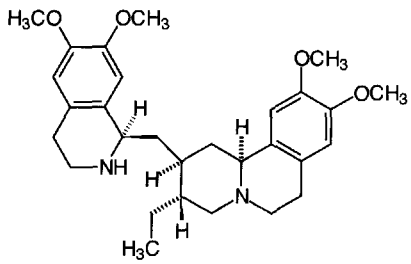
potent emetic and used as an expectorant and antiamoebic agent. It inhibits protein synthesis by preventing translocation of peptidyl-tRNA from the A- to the P-site on the ribosome.



emf *or* **EMF** *abbr. for* electromotive force.

EMG *abbr. for* electromyogram.

+emia *or (esp. Brit.)* **+aemia** *suffix* denoting blood, especially some abnormal condition of the blood.

emilin *abbr. for* elastin microfibril interface located protein; an extracellular matrix glycoprotein, gp115. It is a component of elastin fibres, preferentially located at the elastin–microfibril interface.

emiocytosis a process whereby a secretory substance is released from a cell; a form of **exocytosis**. A secretory granule moves to the cell surface, where the membrane sac enclosing the granule fuses with the plasma membrane, ruptures, and liberates the granule into the extracellular space.

emission *(in physics)* the release of energy in the form of radiation or particles.

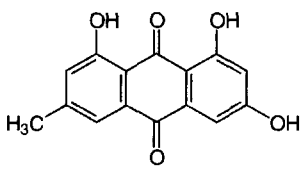
emission spectrophotometry *or* **emission photometry** the processes of measuring an **emission spectrum**, either photometrically or photographically.

emission spectroscopy the **spectroscopy** of an **emission spectrum**. This differs from emission spectrophotometry in being a generic term. Thus measurement may be photometric or photographic, for example.

emission spectrum any **spectrum** of emitted electromagnetic radiation produced by a sample after its atoms or molecules have been put into excited states by the absorption of energy, each line in the emission spectrum being produced by the decay of a particular species of excited atom or molecule to some lower energy level. The exciting energy may be supplied as heat, bombardment by particles, or irradiation with other electromagnetic radiation. *Compare* **absorption spectrum**, **excitation spectrum**.

EMIT *abbr. and trademark for* enzyme-multiplied immunoassay technique; *see* **homogeneous enzyme immunoassay**.

emodin 1,3,8-trihydroxy-6-methylanthraquinone; a compound found (as its rhamnoside) in rhubarb root and other plants.



EMPIGEN BB *proprietary name for* **dodecyl-*N,N*-dimethylglycine**.

EMR *abbr. for* **1** equi-effective molarity concentration ratio. **2** *or* **emr** electromagnetic radiation.

emu *or* **EMU** *abbr. for* electromagnetic unit.

emulsifier **1** *an alternative name for* **emulsifying agent**. **2** a machine for making emulsions.

emulsify to form or to convert into an **emulsion**. —**emulsifiable** *or* **emulsible** *adj.*; **emulsification** *n.*

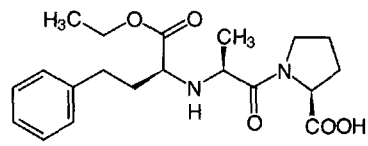
emulsifying agent *or* **emulsifier** any amphiphile or surfactant, such as a phospholipid or a soap, small quantities of which promote the formation of, and stabilize, an **emulsion**.

emulsin a ferment (i.e. an enzyme preparation) obtained from sweet or bitter almonds and originally studied in 1837 by the German chemists Justus von Liebig (1803–73) and Friedrich Wöhler (1800–82) for its ability to degrade **amygdalin**. Together with invertin, it played an important role in **Fischer's** work on enzyme specificity leading to his **lock and key model**. In modern terms, it was an enzyme mixture containing mainly β-glucosidase activity (EC 3.2.1.21).

emulsion **1** a temporary or permanent dispersion of an oil or other hydrophobic material in an aqueous solution, or vice versa, forming an **oil-in-water emulsion** or a **water-in-oil emulsion** respectively. **2** *short for* **photographic emulsion**.

en+ *or (sometimes before b, m, and p)* **em+** *prefix* **1** *(forming verbs)* put in or into, e.g. encapsulate, encode; surround or cover with, e.g. enmesh; to make into a certain condition, e.g. enrich. **2** *(forming nouns and adjectives)* in, into, e.g. endemic.

enalapril (*S*)-1-[*N*-[1-(ethoxycarbonyl)-3-phenylpropyl]-L-alanyl]-L-proline; an inhibitor of **angiotensin converting enzyme** (ACE) and a valuable antihypertensive drug. It has the advantage over **captopril** that it is more easily absorbed and has fewer side effects, and also that enalaprilate, to which it is converted after absorption by removal of the ethyl ester group, is a much more potent ACE inhibitor than captopril. ACE inhibitors were developed from compounds such as succinylproline, an early inhibitor. Conversion of the free succinyl carboxyl group to a sulfhydryl, and addition of a methyl group, yielded captopril with greatly enhanced binding properties. In enalaprilate there was addition of further binding affinity by a phenylethyl group, restoration of carboxyl in place of sulfhydryl and introduction of a secondary amino group. These drugs lower angiotensin II levels which lowers blood pressure, both because of a reduction in direct action of angiotensin as a vasoconstrictor and also by reducing its actions in stimulating aldosterone and norepinephrine release, both of these latter substances having hypertensive effects.



enamel the hard, white, calcified material that forms the outer covering of the crown of a tooth.

enamilin *see* **tuftelin**.

enamine *or* **alkenylamine** any organic molecule having the general structure $R^1R^2NCR^3{=}CR^4R^5$ (where the R groups may be any hydrocarbyl group or H, and the same or different).

enanthate *see* **heptanoate**.

enantiomer either of a pair of **stereoisomers** whose molecules as a whole display **chirality**, i.e. are mirror images of each other and thus not superposable. They are sometimes referred to as optical isomers or optical antipodes; these terms are not recommended. *See also* **enantiomorph** (def. 2), **racemate** (def. 1). *Compare* **diastereoisomer**.

enantiomeric of, or pertaining to, an **enantiomer**; pertaining to the phenomenon of, or displaying **enantiomerism**. Chiral groups that are mirror images of one another are termed **enantiomeric groups**. *See also* **enantiomorphic**, **racemic**.

enantiomeric purity a measure of the proportion of one enantiomer in an enantiomeric mixture expressed as either a fraction or a percentage. *Distinguish from* **optical purity**.

enantiomerism the phenomenon of the existence of **enantiomers** in general, or the existence of enantiomeric molecules in a particular instance; it includes **optical isomerism**.

enantiomorph **1** either of two objects, especially crystals, that

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are mirror images of each other and thus are not superposable. **2** either of the two crystalline forms exhibited by a pair of enantiomers. Use of the term to mean **enantiomer** is deprecated.

enantiomorphic *or* **enantiomorphous** of, or pertaining to, an **enantiomorph**; pertaining to the phenomenon of, or displaying **enantiomorphism**. The term is often used synonymously with **enantiomeric** (enantiomeric molecules frequently form enantiomorphic crystals).

enantiomorphism the phenomenon of being related as between an object and its nonsuperposable mirror image. The term is used especially in relation to enantiomorphic crystals.

enantiomorphous *see* **enantiomorphic**.

enantiotopic **1** when chemically-like ligands in constitutionally equivalent locations (generally the two *a* ligands in *Caabc*) are related by a centre or plane of symmetry, or by an alternating axis of symmetry (but not by a simple axis of symmetry), they are enantiotopic. The two ligands are in a stereochemically different, mirror-image environment. If each *a* ligand of *Caabc* is replaced separately by a different, achiral ligand, *d*, the products are the two enantiomers of *Cabcd*. Example: the methylene hydrogens of ethanol are enantiotopic; if ethanol is written as a Fischer projection structure with OH at the top, H–C–H in the middle, and CH_3 at the bottom, the left-hand hydrogen of the central methylene is H_S, while that at the right is H_R (*see* ***pro-R*/*pro-S* convention**). Replacement of ^1H_R by ^2H yields (+)-(*R*)-[1-$^2H_1$]ethanol and the same replacement of ^1H_S yields the enantiomer, (–)-(*S*)-[1-$^2H_1$]ethanol. In another important compound, citric acid, the two CH_2COOH groups are also enantiotopic. **2** the two faces of a double bond or of a planar cyclic ring system that are related by a symmetry plane but not by a C_2 axis (i.e., a two-fold axis of symmetry) are enantiotopic; the two faces show stereochemically different, mirror-image related environments. Separate addition of the same achiral reagent to the two faces (*see* ***Re*/*Si* convention**) gives enantiomeric products. Example: the simple addition of HCN to CH_3–CHO yields a racemic mixture of the (*R*) and (*S*) cyanohydrins, CH_3–CH(OH)–CN, with both faces of C=O being involved. The reduction of the C=O bond of CH_3–CHO to form ethanol by alcohol dehydrogenase requires addition of a hydride ion from NADH at the C atom and a hydron at the O atom. Thus, reduction of CH_3–CHO with NAD^{2}H at its *A* face (*see* **diastereotopic** (def. 2)) yields (*R*)-[1-$^2H_1$]ethanol and reduction of CH_3–C^{2}HO with *A*-NADH yields (*S*)-[1-$^2H_1$]ethanol. The enzymatic reduction is stereospecific and only one of the enantiotopic faces of C=O is attacked; it is the same one (the *Re* face) in both of these situations. *Compare* **diastereotopic**.

encapsidate to surround (a particle of viral nucleic acid) with a **capsid**. —**encapsidation** *n*.

encapsis the association of myofibrils into bundles and the further association of these bundles into larger bundles, etc.

encephalin *a variant spelling of* **enkephalin**.

encephalitis inflammation of the brain.

3′ end the end of a linear polynucleotide strand at which the 3′-hydroxyl group of the terminal nucleoside residue is normally not phosphorylated.

5′ end the end of a linear polynucleotide strand at which the 5′-hydroxyl group of the terminal nucleoside residue is normally phosphorylated.

end+ *a variant form of* **endo+** *(sometimes before a vowel)*.

end capping *(in chromatography)* the blocking of residual silanol groups on the surface of silica where these remain exposed after the bonding of C_{18} or other alkyl chains to the silica in the formation of reversed-phase stationary phases for column chromatography. For this purpose hydrocarbyl silanes (*see* **silane** (def. 3)) having small alkyl (usually methyl) groups are used so that they can penetrate between the main bonded-phase groups.

endemic present in or peculiar to a more or less localized area, e.g. an endemic disease. *Compare* **enzootic**.

endergonic describing a process or reaction on which work must be done, i.e. one requiring an energy input, for it to take place. At constant pressure and temperature the free energy content of such a system increases. *Compare* **exergonic**. [From **endo+** plus Greek *ergon*, work.]

end group any residue at an extremity of a branched or linear macromolecule.

end-group analysis determination of both the nature and the number of terminal groups in a macromolecule, e.g. in proteins, the N- and C-terminal amino-acid residues; in polynucleotides, the 3′- and 5′-terminal nucleotide residues.

endo+ *or (sometimes before a vowel)* **end+** *comb. form* meaning within, inner, absorbing, containing. *Compare* **exo+**. *See also* **intra+**.

endo- *prefix (in chemical nomenclature)* denoting insertion (of the additional constituent(s) specified) into the structure of (a named compound); e.g. endo-4a-glycine-[5-leucine]enkephalin; endo-Gly^{4a}-[Leu^5]enkephalin; Tyr-Gly-Gly-Phe-Gly-Leu; a synthetic polypeptide in which a glycine residue has been inserted between residues 4 and 5 of [5-leucine]enkephalin.

endo- *prefix (in stereochemistry)*. *See* **conformation**.

endoamylase any **amylase** that hydrolyses nonterminal glycosidic linkages; it is a subcategory of **endoglycosidase**.

endocrine **1** describing or relating to any gland or other group of cells that synthesizes **hormones** and secretes them directly into the blood, lymph, or other intercellular fluid. **2** describing or relating to a secretion of endocrine tissue. **3** a secretory product of endocrine tissue; a hormone. Originally known as **internal secretion**. *Compare* **exocrine**.

endocrine gland *or* **ductless gland** any of the ductless glandular structures that secrete (one or more) hormones directly into the bloodstream.

endocrinology the science concerned with the endocrine organs, their products, and the effects of these products. —**endocrinological** *adj*.

endocytic **1** situated within a living cell but not belonging to the cell itself; intracellular. **2** *an alternative term for* endocytotic (*see* **endocytosis**).

endocytosis the uptake of external materials by cells through the mechanism of **phagocytosis** or **pinocytosis**. The term is often used interchangeably with pinocytosis. *Compare* **exocytosis**, **transcytosis**. *See also* **internalize**, **viropexis**. —**endocytic** *or* **endocytotic** *adj*.; —**endocytose** *vb*.

endocytotic vesicle *see* **pinocytotic vesicle**.

endodeoxyribonuclease *see* **deoxyribonuclease**.

endoenzyme **1** any intracellular enzyme. *Compare* **ectoenzyme**, **exoenzyme** (def. 1). **2** any enzyme that catalyses **endohydrolysis**. It may be an **endoglycosidase**, an **endonuclease**, or an **endopeptidase**. *Compare* **exoenzyme** (def. 2).

endogenous arising or developing within an organism, tissue, or cell, and excluding any consequences of externally added agents or materials. —**endogenously** *adv*.

endoglin a major glycoprotein of vascular endothelium that may be important in the binding of endothelial cells to integrins. It forms a heteromeric complex with the signalling receptors for transforming growth factor β (TGF-β). It has an **RGD** integrin-recognition motif and is a homodimer of disulfide-linked subunits. Example (precursor) from *Sus scrofa*: database code EGLN_PIG, 653 amino acids (70.20 kDa).

endoglycosidase any enzyme within subclass EC 3.2, glycosidases, that hydrolyses nonterminal glycosidic linkages in oligo- or polysaccharides. Many activities of this type are known, e.g. from *Flavobacterium meningosepticum*.

endohormone any hormone acting within the individual organism that produces it. *Compare* **ectohormone**.

endohydrolysis the hydrolysis, esp. by an **endoenzyme**, of any linkage between residues in a biopolymer. For example, **endopeptidases** attack neither the C-terminal nor the N-terminal peptide linkages of an oligo- or polypeptide, and **endoglycosidases** attack the terminal glycosidic linkages at either the reducing or nonreducing end of an oligo- or polysaccharide.

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endolyn-78 a glycoprotein, M_r 78 000, present in substantial amounts in membranes of endosomes and lysosomes, but occurring only at low levels in plasma membrane and the peripheral tubular endosomal compartment.

endomembrane system a hypothetical integrated membrane system of eukaryotic cells, proposed by Morré and Mollenhauer, that represents a developmental and functional continuum. It comprises the endoplasmic reticulum, nucleus, Golgi apparatus and vesicles, plasmalemma, tonoplast, and outer membranes, but not the inner membranes of the mitochondria and chloroplasts.

endometrium the mucous membrane that lines the uterus. It becomes progressively thicker and more glandular in the later stages of the estrous (menstrual) cycle, which prepares it for embryo implantation. If pregnancy occurs the endometrium becomes the decidua, which is shed after birth. If pregnancy does not occur the endometrium returns to its original state; in primates, including humans, much of the endometrium breaks down and is lost in menstruation. —**endometrial** *adj.*

endomitosis the replication of chromosomes without cellular or nuclear division. It is a form of polyploidization that is fairly common in differentiated or differentiating tissues. It is characterized by an increase in nuclear DNA content.

endonuclease any enzyme of a large group of phosphoric diester hydrolases, forming sub-subclasses EC 3.1.21–31, that catalyses the hydrolysis of nonterminal diester linkages in polynucleotides to yield oligonucleotides. Examples include certain of the **deoxyribonucleases** and **ribonucleases**. *Compare* **exonuclease**. *See also* **restriction endonuclease**.

endopeptidase *or* **endoproteinase** *or (formerly)* **proteinase** any enzyme within subclass EC 3.4, peptide hydrolases, that hydrolyses nonterminal peptide linkages in oligopeptides or polypeptides, and comprising any enzyme of sub-subclasses EC 3.4.21–99. They are classified according to the presence of essential catalytic residues or ions at their active sites. Four distinct sub-subclasses are: (1) serine proteinases (EC 3.4.21); (2) cysteine proteinases (EC 3.4.22); (3) aspartic proteinases (EC 3.4.23), and (4) metalloproteinases (EC 3.4.24). There are two major families of serine proteinases, the **chymotrypsins** and the **subtilisins**. Aspartic proteinases contain two aspartic residues at their active site. The metalloproteinases contain metal ions, usually zinc. The proteinases can be distinguished by inhibitors, which are usually specific for a particular class or type.

endopeptidase La the enzyme EC 3.4.21.53; *other names*: ATP-dependent serine proteinase; ATP-dependent protease La; a serine proteinase that catalyses the hydrolysis of large proteins such as globin, casein, and denatured serum albumin in the presence of ATP. It is seemingly the sole member of its own superfamily. Example from *Escherichia coli*: database code JN0303, 784 amino acids (87.35 kDa).

endoperoxide a cyclic peroxide formed from a long-chain polyunsaturated fatty acid, especially arachidonic acid, through the action of **prostaglandin-endoperoxide synthase**.

endoplasm the inner, relatively fluid, part of the **cytoplasm**. *Compare* **ectoplasm**. —**endoplasmic** *adj.*

endoplasmic reticulum *abbr.*: ER; the irregular network of unit membranes, visible only by electron microscopy, that occurs in the cytoplasm of many eukaryotic cells. The membranes form a complex meshwork of tubular channels, which are often expanded into slitlike cavities called **cisternae**. The ER takes two forms, rough (or granular), with ribosomes adhering to the outer surface, and smooth (with no ribosomes attached). When cells are disrupted by homogenization, the cisternae of rough ER break up into small closed vesicles called rough **microsomes**. Similarly the smooth ER may give smooth microsomes. The functions of the two forms of the ER differ. The ribosomes attached to the rough ER are the site of translation of the mRNA for those proteins which are either to be retained within the cisternae (**ER-resident proteins**), the proteins of the **lysosomes**, or the proteins destined for export from the cell. Glycoproteins also undergo their initial glycosylation within the cisternae. The smooth ER has several distinct roles. It is the recipient of the proteins synthesized in the rough ER. Those proteins to be exported are passed to the Golgi complex (*see* **Golgi apparatus**), the resident proteins are returned to the rough ER and the lysosomal proteins after phosphorylation of their **mannose** residues are passed to the lysosomes. Glycosylation of the glycoproteins also continues. The smooth ER is the site of synthesis of lipids, including the phospholipids. The major membrane phospholipids are phosphatidylcholines, phosphatidylethanolamines, phosphatidylserines, and sphingomyelins. The ER also produces cholesterol, triacylglycerols, and ceramides. The membranes of the smooth ER also contain enzymes that catalyse a series of reactions to detoxify both lipid-soluble drugs and harmful products of metabolism. Large quantities of certain compounds such as phenobarbital cause an increase in the amount of the smooth ER.

endoproteinase *or (formerly)* **proteinase** *an alternative name for* **endopeptidase**.

ENDOR *abbr. for* electron nuclear double resonance.

endorphin any endogenous peptide with morphine-like activity. The term was originally applied to a general class of substances of morphine-like activity postulated to occur in the brain; 'endogenous opioid' is now used to denote any peptide, found in higher organisms, that has morphine-like activity. The group includes the pentapeptide **enkephalins**, but the term is most often applied to the endogenous opioid peptides of the pituitary gland, including α-endorphin, which has the structure Tyr-Gly-Gly-Phe-Met-Thr-Ser-Glu-Lys-Ser-Gln-Thr-Pro-Leu-Val-Thr; γ-endorphin has the same structure but with an additional Leu at the C terminus; β-endorphin has the same structure as α-endorphin with additionally -Leu-Phe-Lys-Asn-Ala-Ile-Ile-Lys-Asn-Ala-His-Lys-Lys-Gly-Gln-OH at the C terminus. Endorphins have the same N-terminal tetrapeptide sequence as the enkephalins. Tissue endorphins are larger polypeptides (about 7 kDa) found in pancreas, placenta, and adrenal medulla. The members of this group of peptides originate from large precursor molecules: preproopiomelanocortin is the precursor of β-endorphin, both in brain and other tissues, and [Met^5]enkephalin; preprodynorphin (preproenkephalin B) is the precursor of dynorphin; [Leu^5]enkephalin is formed from preproopiomelanocortin and from preproenkephalin A. *Compare* **exorphin**. [From endo(genous) + morphine.]

endo-α-sialidase EC 3.2.1.129; *other names*: endo-*N*-acetylneuraminidase; endoneuraminidase; poly(α-2,8-sialosyl) endo-*N*-acetylneuraminidase; an enzyme that catalyses the endohydrolysis of α-2,8-sialosyl linkages in oligo- or poly(sialic) acids. Example from bacteriophage k1f: database code ENAN_BPK1F, 919 amino acids (101.77 kDa).

endoskeleton any skeleton lying within an organism, such as the axial skeleton of vertebrates. *Compare* **exoskeleton**.

endosmosis the osmotic flow of water or of an aqueous solution into a cell, organism, or vessel from a surrounding aqueous medium. *Compare* **exosmosis**. —**endosmotic** *adj.*

endosome a membrane-bound organelle in animal cells that carries materials newly ingested by **endocytosis**. It passes many of the materials to lysosomes for degradation.

endosperm the nutritive tissue, found in the seeds of most angiosperms, that surrounds and nourishes the embryo.

endosperm albumin the proteins occurring in the endosperm of, e.g. barley; *see* **protein Z**.

endospore **1** an asexual spore formed within a cell, especially one produced by some bacteria and algae. **2** *or* **endosporium** the innermost coat of the wall of a spore or pollen grain.

endosymbiont a partner in a symbiotic relationship that penetrates the tissues or cells of the other partner; e.g. any of the nitrogen-fixing species of bacteria that occur in the root nodules of legumes. *See* **symbiosis**. *Compare* **ectosymbiont**.

endosymbiotic infection an infection of cells by viruses that replicate without cytopathic effect.

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endothelial leukocyte adhesion molecule *abbr.*: ELAM; *another name for* **selectin**.

endothelin *abbr.*: ET; any one of three 21-residue peptides, called endothelins 1, 2, and 3 (*abbr.*: ET-1, ET-2, ET-3). Endothelins 2 and 3 are so named because of homology with ET-1, which is known to be made by the endothelial cell. ET-1 is the most potent vasopressor compound yet discovered, being ten times more potent than angiotensin II. All three compounds have two disulfide bridges, between cysteine residues 1 and 15, and 3 and 11; these hold the structure in a conical spiral shape. The amino-acid sequence of ET-1 is {bicyclic(1→15, 3→11)}[Cys^1-Ser-Cys^3-Ser-Ser-Leu-Met-Asp-Lys-Glu-Cys^{11}-Val-Tyr-Phe-Cys^{15}-His-Leu-Asp-Ile-Ile-Trp]; ET-2 differs in having -Trp-Leu- at positions 6,7; ET-3 has the substitutions (position in parentheses) Thr(2), Phe(4), Thr(5), Tyr(6), Lys(7), and Tyr(14). The endothelins are products of three distinct genes, and are synthesized as part of a large precursor molecule, **preproendothelin** (prepro-ET), which is then proteolytically processed. The 2.2 kb mRNA for human prepro-ET-1 is encoded in five exons, the 5′-flanking region containing response elements for phorbol ester (Fos/Jun-inducible) and nuclear factor 1 (TGF-β-induced expression; *see* **transforming growth factor**), and its expression is stimulated by vasopressor hormones such as epinephrine, angiotensin II, and arginine vasopressin, as well as TGF-β (from aggregating platelets), thrombin, and interleukin-1. Prepro-ET-1 is a 203-residue peptide, which is cleaved to the 92-residue pro-ET (**big endothelin**), from which ET-1 is formed by **endothelin converting enzyme**. Related peptides are **vasoactive intestinal contractor** and **sarafotoxin**, a peptide produced by *Atractaspsis engaddensis*. Only ET-1 is detected in vascular endothelial cells; it is also expressed in nonvascular cells in other tissues, including brain, kidney, and lung. ET-2 and ET-3 are expressed in tissues such as brain, kidney, adrenal, and intestine.

endothelin receptor any of several membrane proteins that bind **endothelins** and mediate their intracellular effects. They are G-protein-coupled seven-transmembrane-domain receptors. The structures of two types have been predicted from human, rat, and bovine cDNA. ET_A (human, 427 amino acids) has affinity ET-1 ⩾ ET-2 ≫ ET-3, while ET_B (human, 442 amino acids) is equipotent for all three.

endothelium the single layer of thin, flattened cells of mesoblastic origin that lines the blood vessels and some body cavities, e.g. those of the heart. *Compare* **epithelium**, **mesothelium**. —**endothelial** *adj.*

endothelium-derived relaxing factor *abbr.*: EDRF; *see* **nitric oxide**.

endothermic describing a process or reaction that absorbs heat, i.e. a process or reaction for which the change in enthalpy, ΔH, is positive at constant pressure and temperature. *Compare* **exothermic**.

endothiapepsin EC 3.4.23.22; *other name*: *Endothia* aspartyl proteinase. An enzyme that catalyses the hydrolysis of proteins with broad specificity similar to that of **pepsin** A; it prefers hydrophobic residues at P1 and P1′, but does not cleave the Ala–Leu linkage in the B chain of insulin or the protected dipeptide Cbz-Glu-Tyr; it clots milk. Example from *Cryphonectria parasitica* (*Endothia parasitica*; chestnut blight fungus): database code NRL_4APE, 330 amino acids (33.76 kDa); 3-*D* structure known; it is similar to other aspartic proteases.

endotoxin any microbial toxin that cannot easily be separated from the structure of the cell. *Compare* **exotoxin**.

end point *or* **endpoint** the point in a titration that should (but may not always) correspond to the theoretical **equivalence point**.

end product the final chemical substance formed in a sequence of metabolic (or chemical) reactions.

end-product inhibition the inhibition of a sequence of metabolic reactions by the end product of the sequence, usually by action on a reaction which is often at the beginning of the sequence.

end-window counter a **Geiger counter** or **proportional counter** so constructed that its base is relatively transparent to the radiation to be detected.

+ene *suffix (in chemical nomenclature)* indicating the presence of one or more carbon–carbon double bonds in an organic compound.

enediol any acyclic organic compound in which there is a hydroxyl group attached to each of two carbon atoms that are linked by a double bond. *Compare* **enol**.

energy *symbol*: *E*; the capacity of a system for doing work. There are various forms of energy – potential, kinetic, electrical, chemical, nuclear, and radiant – which can be interconverted by suitable means. The SI unit of energy is the joule.

energy balance the algebraic balance of the various energy inputs versus energy outputs of a system; it is positive if energy is released and negative if it is absorbed. In physiology it is the relation of the amount of energy taken into the organism to the amount used for internal work, external work, and for the growth and repair of tissues.

energy barrier *see* **potential energy barrier**.

energy charge *see* **adenylate energy charge**.

energy coupling the coupling of ATP synthesis to electron transport in the **respiratory chain**.

energy diagram a diagram representing the energy contents of various states of the reactants, activated complexes, and products in a chemical reaction; or of the nuclear energy levels of an atom; or of the electronic energy levels of an atom or molecule.

energy flow *(in ecology)* the transfer of energy between organisms in an ecosystem.

energy level any of the stable energy states that a molecular entity can take up. In **quantum mechanics** only certain discrete energy levels are possible and continuous variation of the energy level of a molecular entity is excluded.

energy metabolism the metabolic reactions of a cell or organism concerned with energy transformations.

energy of activation *see* **activation energy**.

energy-poor *term sometimes used to describe* **1** a compound whose hydrolysis under standard conditions manifests a small negative free energy change. *See also* **low-energy compound**. **2** a chemical group with a low **group potential**. **3** the linkage of such a chemical group to some other group.

energy requirement the amount of energy needed to maintain a cell or organism.

energy sink a molecule or a group in a molecule that is able easily to accept energy transferred to it from another component of the system.

energy transduction *see* **transduction** (def. 2).

energy transfer the transfer of excitation energy from one chromophore or one molecular entity to another by a process not involving radiation; the energy may then be dissipated in a variety of ways, e.g. by fluorescence. Such energy transfer is very dependent on the distances involved and is useful in studies of structural relationships between groups on a macromolecule.

energy trapping the processes by which energy released in a catabolic reaction is coupled to the synthesis of another compound, often a nucleoside triphosphate such as ATP.

engineered **1** (of a cell or organism, or a strain of cells or organisms) *colloquial term for* **genetically engineered**. **2** (of a nucleotide sequence) *jargon term, usually followed by 'into'* artificially inserted (into a longer sequence, such as a vector). **3** (of a protein) *jargon term* describing an altered protein synthesized by a cell or organism (or a strain of cells or organisms) whose genetic material has been manipulated to that end.

engrailed any of various protein products of the **homeotic gene** *engrailed*; in *Drosophila* this is a segment-polarity gene. Examples: engrailed-1 and engrailed-2 (human) respectively: database codes HME1_HUMAN and HME2_HUMAN, 391 amino acids (40.00 kDa) and 332 amino acids (34.12 kDa); en-

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grailed chain C, *Drosophila melanogaster*, database code NRL_1HDDC, 57 amino acids (6.94 kDa); 3-D structure of complex with DNA known; one motif.

enhancement **1** the improvement of the effects of ionizing radiation on tissue by dioxygen or other chemical agents. **2** the increased yield of one virus from cells infected by another virus; the term is often used when the mechanism of the process is not known. *Compare* **complementation** (def. 2), **interference**. **3** *see* **Emerson enhancement**. **4** *see* **fluorescence enhancement**.

enhancement of fluorescence *an alternative term for* **fluorescence enhancement**.

enhancement spectrum a spectrum showing the enhancement of photosynthetic **quantum yield** from that produced at a fixed-wavelength background illumination to that produced by illumination with a variable-wavelength beam. Such spectra show peaks that can sometimes be reasonably well identified with specific pigments in the system. *Compare* **Emerson enhancement**.

enhancer *(in molecular biology)* a eukaryotic control element that can increase expression of a gene. Enhancers may be located some distance from the gene and may be either upstream or downstream.

enhancesome a disclike structure, formed by a 180 bp loop of DNA and dimers of the *Xenopus* transcription factor xUBF, that is involved in rRNA transcription.

enkephalin any pentapeptide **endorphin** with the sequence Tyr-Gly-Gly-Phe-Xaa. There are two similar naturally occurring enkephalins, present in brain, spinal cord, and gut; their recommended trivial names are: [5-leucine]enkephalin (*abbr.*: [Leu^5]enkephalin *or* [Leu]enkephalin), Tyr-Gly-Gly-Phe-Leu (I); and [5-methionine]enkephalin (*abbr.*: [Met^5]enkephalin *or* [Met]enkephalin), Tyr-Gly-Gly-Phe-Met (II). (II has the same sequence as residues 61–65 of β-**lipotropin**.) The common precursor of I and II, proenkephalin – itself formed from preproenkephalin by removal of the signal peptide – contains four copies of II and one each of I, the heptapeptide [Met^5]enkephalinyl-Arg-Phe, and the octapeptide [Met^5]-enkephalinyl-Arg-Phe-Leu. (*Note*: Designations such as Leu-, leucyl-, or leucine-enkephalin have commonly been given to I, with corresponding terms for II, but all of these incorrectly imply N-terminal extension with a residue of leucine or methionine, respectively.)

enkephalinase *see* **carboxypeptidase H**.

enkephalin convertase a specific carboxypeptidase that converts enkephalin precursors into enkephalin in adrenal chromaffin granules. It is now known as **carboxypeptidase H**.

enniatin any of various antibiotics from *Fusarium* spp. that function as **ionophores**. They are cyclodepsipeptides (*see* **depsipeptide**).

enol any acyclic organic compound with a hydroxyl group attached to either of two carbon atoms that are linked by a double bond. *Compare* **enediol**. *See also* **keto–enol tautomerism**.

enolase EC 4.2.1.11; *recommended name*: phosphopyruvate hydratase; *other name*: 2-phosphoglycerate dehydratase. An enzyme that catalyses the conversion of 2-phospho-D-glycerate to phospho*enol*pyruvate and H_2O; magnesium is a cofactor. Example from *Saccharomyces cerevisiae*: database code NRL_7ENL, 436 amino acids (46.58 kDa); 3-D structure known; six motifs.

enology *or (esp. Brit.)* **oenology** the study of wines.

5-enolpyruvylshikimate-3-phosphate phospholyase *see* **chorismate synthase**.

eNOS *see* **nitric-oxide synthase**.

enoyl an acyl group derived from any alkenoic acid.

enoyl-[acyl-carrier protein] reductase (NADPH, A-specific) EC 1.3.1.39; *other name*: acyl-ACP dehydrogenase; an enzyme of the **fatty acid synthase complex** in liver. It catalyses the reduction by NADPH of *trans*-2,3-dehydroacyl-[acyl-carrier protein] to form acyl-[acyl-carrier protein] and $NADP^+$.

enoyl-CoA hydratase **1** EC 4.2.1.17; *systematic name*: (3*S*)-3-hydroxyacyl-CoA hydro-lyase; *other names*: enoyl hydrase, unsaturated acyl-CoA hydratase; an enzyme of the **beta-oxidation system**, present in mitochondria and peroxisomes. It catalyses the hydration of (3*S*)-3-hydroxyacyl-CoA to *trans*-2(or 3)-enoyl-CoA. It is a mitochondrial matrix protein, a homohexamer; a characteristic transit peptide sequence is found in the precursor. Example (precursor) from rat: database code ECHM_RAT, 290 amino acids (31.48 kDa). **2** EC 4.2.1.74; *recommended name*: long-chain-enoyl-CoA hydratase; an enzyme that catalyses a similar reaction to the above; it does not act on crotonoyl-CoA. *See also* **beta-oxidation system**.

enoyl-CoA isomerase *see* **dodecenoyl-CoA Δ-isomerase**.

3,2-*trans*-enoyl-CoA isomerase *see* **dodecenoyl-CoA Δ-isomerase**.

enrich to increase in content or abundance; e.g. to increase the abundance of one (usually stable) nuclide of an element above its naturally occurring level; to increase the content in a foodstuff of one or more specific nutrients (such as vitamins or minerals) above the natural level. —**enrichment** *n.*

enrichment medium a selective culture medium that favours the growth of a desired microorganism.

entactic describing an enzyme poised for catalytic action in the absence of substrate.

entactin *or* **nidogen** a sulfated Ca^{2+}-binding protein occurring in basement membrane and involved in cell adhesion; it binds **laminin** and type IV collagen. The protein has two globular domains, an **EF-hand** domain, EGF-like domains and a thyroglobulin type I domain. Example (precursor) from human: database code NIDO_HUMAN, 1247 amino acids (136.34 kDa).

enteric *or* **enteral** of or pertaining to the intestine or gut.

enteric-coated describing a drug or medicament that is prepared in a form enabling it to pass through the stomach unaltered and be released in the intestine.

entero+ *or (before a vowel)* **enter+** *comb. form* denoting the intestine.

enterobactin *or* **enterochelin** *N′,N′,N″*-tris(2,3-dihydroxybenzoyl)-2,6,10-trioxo-1,5,9-trioxacyclododecane-3,7,11-triamine; a **siderochrome** of the catechol-derivative variety produced by certain members of the Enterobacteriaceae, e.g. *Escherichia coli*, *Salmonella* spp. It is the cyclic self-triester (trilactide) of *N*-(2,3-dihydroxybenzoyl)-L-serine, and a product of the **shikimate pathway**.

enterochelin *an alternative name for* **enterobactin**.

enterochromaffin cell *abbr.:* EC cell; any gut endocrine cell containing biogenic monoamines that gives a positive **chromaffin** reaction and displays a characteristic yellow formaldehyde-induced fluorescence. Such cells may be divided immunocytochemically and ultrastructurally into functionally distinct types.

enterocrinin a putative peptide hormone, crystallizable from extracts of intestine of certain mammals, that is held to stimulate duodenal and jejunal secretion of digestive enzymes.

enterocyte any of the columnar epithelial cells on the luminal surface of the villi of the small intestine. Enterocytes are immature in the crypts, mature in the middle of the villi, and senile at the exfoliation area at the villous tips. They have numerous microvilli on their luminal surface (the brush border) and are responsible for the synthesis of digestive enzymes and for the absorption of materials from the gut.

enterogastrone the putative hormone from the duodenum that inhibits gastric activity. Some or all of the actions attributed to enterogastrone are probably due to **glucose-dependent insulinotropic peptide**.

enterogastrone effect *see* **gastric inhibitory peptide**.

enteroglucagon a collective term for a small family of peptides derived from **proglucagon** by post-translational processing in the L cells (or **EG cells**) of the distal small intestine and colon. One component is GLP-$1^{7\ 37}$ (*see* **GLIP**).

enteroglucagon *or* **glucagon-37** *or* **oxyntomodulin** a peptide isolated from porcine jejuno-ileum that interacts with glucagon receptors and activates adenylate cyclase in hepato-

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cytes. It has a specific action on the acid-secreting area of gastric mucosa. It has 37 residues, of which the sequence of the N-terminal 29 is identical with that of pancreatic glucagon.

enterohepatic recirculation the cycle of secretion from the gall bladder into the upper intestinal tract with reabsorption in the lower tract and transport to the liver followed by resecretion. *See* **bile acids**.

entero-insular axis the interrelationship of endocrine function between the gastrointestinal tract and the pancreatic islets in which signals arising in the gut after ingestion of nutrients effect endocrine responses by the islets.

enterokinase *a former name for* **enteropeptidase**.

enteropeptidase *or (formerly)* **enterokinase** the enzyme EC 3.4.21.9; a serine proteinase enzyme of the brush border of the upper small intestine that activates **trypsinogen** by the selective cleavage of the Lys^6-|-Ile^7 bond in the latter. Example (precursor) from *Bos taurus*: database code ENTK_BOVIN, 1035 amino acids (114.89 kDa); residues 1–800 form the non-catalytic heavy chain, 801–1035 the catalytic light chain.

enterotoxin any bacterial **exotoxin**, whether ingested or produced within the intestine, that has an action upon the intestinal mucosa, usually giving rise to diarrhoea and other unpleasant symptoms. **Cholera toxin** is an example. Other enterotoxins are produced by *Escherichia coli* and some Staphylococci. Of the *E. coli* enterotoxins, LT (from labile, i.e. heat-labile, toxin) is similar in structure to cholera toxin and has a similar mode of action. ST (from heat-stable toxin) has an effect similar to atrial **natriuretic peptide**, activating guanylate cyclase. It has 13 amino acids. Other enterotoxins produced by *E. coli* include **hemolysin** and vero toxin, a Shiga-like toxin similar to that of *Shigella dysenteriae* that has *N*-glycosidase activity, and cleaves an adenine residue from the 28S rRNA of the 60S ribosome subunit.

enthalpimetry the measurement of the **enthalpy** of a body or system.

enthalpy *or* **heat content** *symbol*: H; a physical quantity and a thermodynamic property defined as the sum of the internal energy of a system, U and the product of the volume, V, multiplied by the pressure, p, i.e. $H = U + pV$. Enthalpy is related to the **Gibbs energy**, G, by the equation $G = H - TS$, where T denotes the thermodynamic temperature and S denotes **entropy**.

Entner–Doudoroff enzyme the 'catabolic' D-glucose-6-phosphate dehydrogenase (EC 1.1.1.49) from *Pseudomonas fluorescens*. It is a 220 kDa protein composed of four, apparently identical, polypeptide chains. *See also* **Entner–Doudoroff pathway**.

Entner–Doudoroff pathway a metabolic pathway occurring in *Pseudomonas* spp. in which D-glucose 6-phosphate is first oxidized to 6-phospho-D-gluconate, which is then acted on by 6-phosphogluconate dehydratase (EC 4.2.1.12) to form 2-dehydro-3-deoxy-6-phospho-D-gluconate. This is then split by 2-dehydro-3-deoxyphosphogluconate aldolase (EC 4.1.2.14) to give pyruvate and D-glyceraldehyde 3-phosphate. [After Nathan Entner (*1920–*) and Michael Doudoroff (*1911–*).]

entomology the science of the study of insects.

entopic occurring in the usual place. *Compare* **ectopic**.

ENTREZ a suite of computer programs accessible via the Internet that links **MEDLINE** with genome and sequence databases.

entropic union a polymerization, or other reaction, resulting from an energetically unfavourable interaction of a surface of the molecule in question with water molecules; the polymerization causes the removal of water from the molecules' surfaces and a hence a decrease in the free energy content of the system.

entropy *symbol*: S; a physical quantity and a thermodynamic property indicating the amount of disorder in a system; i.e. the amount of energy in a system that is unavailable for doing work. In any irreversible process the total entropy of all systems concerned is increased. In a reversible process the total increase in entropy in all systems concerned is zero, while the increase in entropy, dS, of any individual system, or part of a system, is equal to the heat that it absorbs, dq_{rev}, divided by the thermodynamic temperature, T; i.e. $dS = dq_{rev}/T$. Entropy is related to **Gibbs energy**, G, and **enthalpy**, H, by the equation $G = H - TS$. The SI unit for entropy is $J\ K^{-1}$ —**entropic** *adj.*

entry exclusion the phenomenon in which a resident plasmid interferes with the entry of genetic material to a cell by (bacterial) **conjugation** (def. 4).

enucleate **1** to remove the nucleus from (a cell). **2** (of a cell) deprived of its nucleus. —**enucleation** *n.*

enuresis the involuntary passing of urine. —**enuretic** *adj.*

env a viral gene for **envelope protein**.

envelope **1** any covering or enclosing structure, e.g. a membrane, capsule, shell, or skin. **2** the cell membrane of a bacterium, together with all the structures external to it including the cell wall and, sometimes, the capsule. **3** *or* **peplos** an outer lipoprotein coat of a virion that occurs in an **enveloped virus**. **4** *see* **nuclear envelope**.

envelope conformation any ***conformation*** of a nonplanar five-membered saturated ring compound when four of its ring atoms lie in one plane and the remaining atom lies outside that plane. For a monosaccharide or monosaccharide derivative the conformational descriptor *-E* may be added to its name.

enveloped virus any virus in which a nucleoprotein core is surrounded by a lipoprotein envelope consisting of a closed bilayer of lipid derived from that of the host cell's membrane(s), with glycoprotein on the outside and matrix protein or nucleocapsid protein on the inside. Enveloped viruses include herpesviruses, negative-strand RNA viruses, retroviruses, and togaviruses.

envelope protein any protein (usually a glycoprotein) of the envelope of a virus. Example: envelope polyprotein gp160 precursor of human immunodeficiency virus (HIV) type 1; database code ENV_HV1A2, 855 residues (97.33 kDa). Residues 1–29 are the signal peptide; 30–509 form exterior membrane glycoprotein gp120; 510–855 form transmembrane glycoprotein gp41. The variable (very rapidly evolving) antigenic regions of HIV are in the gp120 sequence.

envelysin EC 3.4.24.12; *other names*: sea-urchin-hatching proteinase; hatching enzyme; an enzyme so named because it dissolves (lyses) the fertilization envelope of the sea-urchin embryo. It is a metalloendopeptidase that catalyses the preferential cleavage of proteins on the amino side of bulky hydrophobic residues, Leu, Ile, Phe, and Tyr. The enzyme requires zinc and calcium. Example (precursor) from the sea urchin *Paracentrotus lividus*: database code HE_PARLI, 587 amino acids (65.14 kDa).

Enzacryl *the proprietary name for* a group of synthetic carriers for the immobilization of enzymes and other organic biomolecules that are copolymers of acrylamide and various derivatives of *N*,*N*′-methylene diacrylamide.

enzootic present in or peculiar to animals in a more or less localized area; e.g. an enzootic disease. *Compare* **endemic**.

enzyme any naturally occurring or synthetic macromolecular substance composed wholly or largely of protein, that catalyses, more or less specifically, one or more (bio)chemical reactions at relatively low temperatures. The action of RNA that has catalytic activity (*see* **ribozyme**) is often also regarded as enzymic. Nevertheless, enzymes are mainly proteinaceous and are often easily inactivated by heating or by protein-denaturing agents. The substances upon which they act are known as **substrates**, for which the enzyme posseses a specific binding or ***active site***. *See also* ***enzyme classification***, ***isoenzyme***. [From German *enzym*, possibly from modern Greek *enzumos*, leavened, or more probably from Greek *en*, in, + *zumē*, leaven, yeast.] —**enzymic** *or* **enzymatic** *adj.*

enzyme I EC 2.7.3.9; enzyme I of the **phosphotransferase** system; phospho*enol*pyruvate–protein phosphotransferase; *systematic name*: phospho*enol*pyruvate:protein-L-histidine N^{π}-phosphotransferase. A soluble bacterial enzyme, part of a system for the transport of hexoses across the cell membrane, that cata-

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lyses the phosphorylation by phospho*enol*pyruvate of a low M_r, heat-stable protein, **HPr**. *Compare* **enzyme II** (def. 1).

enzyme II **1** EC 2.7.1.69; enzyme II of the **phosphotransferase** system; protein-N^{π}-phosphohistidine–sugar phosphotransferase; *systematic name*: protein-N^{π}-phosphohistidine:sugar N^{π}-phosphotransferase. Any of a group of related membrane-bound bacterial enzymes, part of the system for the transport of hexoses across the cell membrane, that catalyse the phosphorylation of hexoses by phospho-HPr (*see* **enzyme I**). Enzyme II is responsible for the specificity of the transport process with respect to the sugar. **2** *a former name for* **acyl-carrier protein**.

enzyme-activated irreversible inhibitor *an alternative name for* **suicide inhibitor**.

enzyme activation the generation of a catalytically active enzyme from an inactive or poorly active form or from a biosynthetic precursor (proenzyme). Activation may be by enzymic or chemical covalent modification or by addition of a specific activator.

enzyme adaptation *see* **inducible enzyme**.

enzyme cascade *see* **cascade sequence**.

enzyme classification the systematic arrangement and naming of enzymes by the **Enzyme Commission**. Each enzyme is denoted by the abbreviation EC followed by a set of four numbers separated by stops. The first number denotes one of the six main divisions: EC 1, oxidoreductases; EC 2, transferases; EC 3, hydrolases; EC 4, lyases; EC 5, isomerases; and EC 6, ligases. The second number denotes the subclass, the third number denotes the sub-subclass; the fourth number is the serial number of the particular enzyme. The most recent edition of the classification, *Enzyme Nomenclature 1992* (IUB/Academic Press; San Diego, London), lists 3196 enzymes.

enzyme cluster *or (sometimes)* **multienzyme cluster** **1** any physiologically significant system of two or more enzymes in physical (i.e. noncovalent) association. The term embraces any **enzyme complex**, **multienzyme complex**, or membrane-bound enzyme array. Clustered enzymes usually display different kinetic and/or regulatory features from their unassociated counterparts; they may be encoded in a cluster-gene. *See also* **multienzyme system**. **2** *an alternative term for* **cluster** (def. 2).

Enzyme Commission *or* **the International Commission on Enzymes**; a body established in 1956 by the International Union of Biochemistry (IUB) to consider the classification and nomenclature of enzymes and coenzymes, their units of activity and standard methods of assay, together with the symbols used in the description of enzyme kinetics. The Commission, which worked closely with the Biological Chemistry Nomenclature Commission of the International Union of Pure and Applied Chemistry (IUPAC), was dissolved in 1961 and its work has been carried on in turn by the Standing Committee on Enzymes of IUB, by the IUPAC/IUB Joint Commission on Biochemical Nomenclature (JCBN), by an Expert Committee on Enzymes, and most recently by the Nomenclature Committees of IUB (NC-IUB) or the International Union of Biochemistry and Molecular Biology (NC-IUBMB). *See also* **enzyme classification**.

enzyme complex an operational term for any structural and functional entity composed of a number of dissociable enzymes that catalyse a sequence of closely related chemical reactions. *Compare* **multienzyme**.

enzyme detergent any detergent preparation incorporating an enzyme to assist its cleansing action. The enzymes used in such detergents are usually proteinases of high thermal and alkaline stability, e.g. **Alcalase**.

enzyme differentiation the process whereby, during the development of an organism, each tissue acquires its own characteristic quantitative pattern of enzymes, which underlies the physiological functions and morphological features of the tissue. From a fairly uniform enzymic make-up in the cells of the early embryo, the enzyme patterns of different tissues become progressively more differentiated as development into the mature organism proceeds.

enzyme electrode any electrode, incorporating an enzyme into its structure, that responds to the concentration of one of the substrates or products of the reaction catalysed by the enzyme. The enzyme is trapped within a gel matrix surrounding the electrode or is kept in contact with the electrode by a semi-permeable membrane.

enzyme engineering *or* **enzyme technology** the branch of biomolecular engineering concerned with processes designed to produce, isolate, purify, and immobilize enzymes and to use them for the catalysis of specific chemical reactions.

enzyme immunoassay *or* **enzymoimmunoassay** *abbr.*: EIA; any **immunoassay** in which an enzyme-catalysed reaction is used as the indicator. *See also* **heterogeneous immunoassay**, **homogeneous immunoassay**.

enzyme induction the synthesis of an enzyme in a cell or organism at a markedly increased rate in response to the presence of an **inducer**. The inducer is thought to combine with a **repressor** thereby preventing the latter from blocking an **operator**, which controls the translation of the structural gene for the enzyme.

enzyme-inhibition immunoassay a variation of **enzyme immunoassay** in which the inhibition of an enzyme-catalysed reaction is used as the indicator.

enzyme labelling a method used to detect or locate (and sometimes estimate) an antigen in, e.g., a tissue section. The section is exposed to a complementary antibody that has been covalently linked to an enzyme; the antibody binds to the antigen, and its location (and its amount) is determined by an assay dependent on the catalytic activity of the linked enzyme. *See also* **enzyme immunoassay**.

enzyme-linked immunosorbent assay *abbr.*: ELISA; a form of quantitative **immunoassay** based on the use of antibodies (or antigens) that are linked to an insoluble carrier surface, which is then used to 'capture' the relevant antigen (or antibody) in the test solution. The antigen–antibody complex is then detected by measuring the activity of an appropriate enzyme that had previously been covalently attached to the antigen (or antibody).

enzyme membrane any (semipermeable) membrane to which an enzyme has been covalently bound. Such membranes are useful in constructing **enzyme electrodes**.

enzyme-multiplied immunoassay technique *abbr. and proprietary name*: EMIT; *an alternative name for* **homogeneous enzyme immunoassay**.

enzyme-paper graft an enzyme immobilized on (filter) paper, which is frequently impregnated with indicators. It is useful for making analytical devices.

enzyme reactor a device for using immobilized enzymes or enzyme systems for synthetic or other processing reactions, especially on an industrial scale.

enzyme recruitment the exploitation of substrate-ambiguous enzymes or transport proteins in the evolution of new biochemical pathways.

enzyme repression inhibition of the formation of an enzyme by a compound formed in or taken in by a cell or organism.

enzyme specificity *see* **specificity**.

enzyme–substrate complex *abbr.*: ES; the stoichiometric complex of an enzyme molecule and a substrate molecule bound at the enzyme's active site.

enzyme technology *an alternative term for* **enzyme engineering**.

enzyme unit *symbol*: U; *abbr.*: EU; an obsolete unit of activity of enzymes, defined as the amount of enzyme that will catalyse the transformation of one micromole of the substrate per minute under standard conditions. It has now been superseded by the **katal**.

enzymic *or* **enzymatic** by, of, involving, or relating to an enzyme or enzymes; catalysed by an enzyme or by enzymes. — **enzymically** *or* **enzymatically** *adv.*

enzymic activity the rate of reaction of substrate that may be attributed to catalysis by an enzyme. The concept is now obsolete, having been superseded by **catalytic activity**. The unit of

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enzymic activity was initially the **enzyme unit** and subsequently the **katal** (as originally defined). The derived quantity concentration of enzymic activity was defined as activity divided by volume and was expressed as katals per litre. *See also* **catalytic activity concentration**, **molar (enzymic) activity**, **specific (enzymic) activity**.

enzymic cycling a form of **catalytic assay** in which there is no coupled indicator reaction; instead, the regenerating system is allowed to cycle for a set time, after which the reactions are stopped by destruction of all enzymes and the most easily determined product is measured in a separate assay. The coupled system thus acts as a chemical amplifier in the determination of the intermediate catalyst.

enzymo+ *comb. form* denoting an **enzyme** or enzymic activity.

enzymoimmunoassay *an alternative name for* **enzyme immunoassay**.

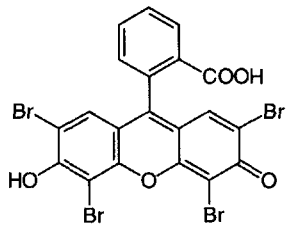
enzymology the science of the study of enzymes and enzyme-catalysed reactions. —**enzymological** *adj.*; **enzymologist** *n.*

enzymolysis the enzyme-catalysed splitting of a chemical compound into smaller ones. The term commonly refers to enzymic hydrolysis. —**enzymolytic** *adj.*

eobiogenesis the first occurrence of the formation of living matter from nonliving material.

eobiont any system showing some characteristics of living systems but not enough to be generally accepted as living.

eosin any of a number of similar red acidic dyes, derivatives of fluorescein, especially Eosin Y (yellowish), 2′,4′,5′,7′-tetrabromofluorescein disodium salt, Acid Red 87 (CI 45380), or Eosin B (bluish), 4′,5′-dibromo-2′,7′-dinitrofluorescein disodium salt, Acid Red 91 (CI 45400). They are widely used as stains in histology and hematology.



2′,4′,5′,7′-tetrabromofluorescein

eosinophil(e) **1** *or* **eosinophil leukocyte** *or* **eosinophilic leukocyte** a polymorphonuclear leukocyte, present in blood and other connective tissues, that has numerous large cytoplasmic granules that stain readily with eosin. The granules contain numerous hydrolytic enzymes including acid phosphatase, arylsulfatase, cathepsins, glucuronidase, peroxidase, and ribonuclease. The relative number of eosinophils in the blood, normally low, rises markedly in certain allergic conditions and parasitic infections but their function is poorly understood. **2** any cell whose cytoplasm stains readily with eosin, especially an eosinophilic cell of the anterior pituitary that secretes prolactin and somatotropin.

eosinophil cationic protein *abbr.*: ECP; a highly basic zinc-containing **ribonuclease** that binds avidly to negatively charged surfaces and is particularly effective at damaging the tegument of schistosomes.

eosinophilic having an affinity for **eosin**.

eosinotactic having an attractive or repulsive action on eosinophils. [A contraction of eosinophil + chemotactic.]

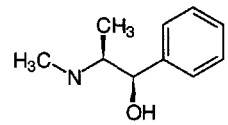
eosome the suggested primary particulate biogenetic precursor, via the **neosome**, of the **ribosome**. Eosomes of *Escherichia coli* have an average sedimentation coefficient of 14S.

EPA *abbr. for* **1** eicosapentaenoic acid. Normally indicating the (all-*Z*)-5,8,11,14,17 isomer. **2** erythroid potentiating activity (*see* **TIMP**).

EpETrE *abbr. for* epoxyeicosatrienoate.

EPH a gene encoding a subfamily of protein tyrosine kinases. It is named from erythropoietin-producing hepatocellular carcinoma cell line, from which the probe used to isolate the gene was obtained. Related proteins are Elk (Eph-like kinase), Eek (Eph and Elk-related kinase), Eck (epithelial cell kinase), and Erk (Elk-related kinase). Overexpressed *EPH* has tumorigenic potential; the ligand of Eph is unknown; database code for the expressed protein: KEPH_HUMAN, 984 amino acids (108.80 kDa); residues 1–23 are the signal 24–984 Eph.

ephedrine (1*R*,2*S*)-1-phenyl-1-hydroxy-2-methylaminopropane; an alkaloid obtained from several species of gymnosperm shrubs belonging to the genus *Ephedra*. A structural analogue of epinephrine, it mimics central and peripheral effects of noradrenergic and adrenergic neurons through direct and indirect actions, hence its CNS-stimulant effects and its use as a decongestant in upper respiratory tract infections.



epi+ *or (before a vowel)* **ep+** *prefix* denoting **1** on, upon, above, over, beside, near, close to, in addition to. **2** a chemical compound or group related in some way to a specified chemical compound or group, e.g. an **epimer**. **3** a chemical compound or group distinguished from a specified chemical compound or group by having a bridge connection in the molecule, e.g. an **epoxide**.

epiarginase *see* **epiprotein**.

epichlorohydrin 3-chloropropylene oxide; chloromethyloxirane; 1-chloro-2,3-epoxypropane; a colourless liquid widely used in industry as a solvent and an intermediate in the manufacture of glycerol, glycerol ethers and epoxy resins. In the presence of potassium hydroxide it reacts with compounds containing alcoholic hydroxyl groups to form diethers of glycerol and hence finds application in the manufacture of cross-linked derivatives of polysaccharides such as the proprietary materials Sephacel, Sephadex, and Sepharose.

epidemic **1** describing a disease that affects many persons simultaneously in a more or less restricted area. **2** the widespread occurrence of a disease in a human population. *Compare* **endemic**.

epidemiology the study of the nature and spread of a disease in a human population.

epidermal growth factor *abbr.*: EGF; any member of a group of heat-stable, hormonal, ≈6 kDa proteins that consist of a single polypeptide chain of 49–53 residues with three intrachain disulfide bonds; they are classified as **cytokines**. One form (mEGF), originally known as tooth-lid factor, can be isolated from submaxillary glands of the male mouse (*see* **nerve growth factor**). A similar protein (hEGF), extracted from human pregnancy urine and named **urogastrone**, is now known to be highly homologous to EGF (37 of 53 residues identical, disulfide bonds preserved). The main effects of EGF *in vivo* are to stimulate the growth of epidermal and epithelial cells, and to inhibit the secretion of gastric acid. It also has a potent mitogenic action on many types of cultured mammalian cells and displays a number of insulin-like properties towards them (*see* **insulin-related growth factors**). It is synthesized as a large preprotein, EGF membrane glycoprotein precursor, which contains, as well as the mature EGF protein, nine EGF-like repeats and urogastrone. Example (precursor) from human: database code EGF_HUMAN, 1207 residues (133.79 kDa). The action of EGF is mediated by the **epidermal growth factor receptor**.

epidermal growth factor receptor *or* **EGF receptor** the mediator of the biological signal of **epidermal growth factor** (EGF)

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and also of **transforming growth factor-α** (TGF-α). It is a membrane protein with a single transmembrane domain, and a **tyrosine kinase** activity in the cytoplasmic domain; the extracellular domain, which binds EGF, is highly glycosylated. The v-*erbB* oncogene codes for a protein highly homologous to a truncated EGF receptor, and the gene that codes for the receptor is now regarded as the protooncogene c-*erbB* (*see* ***erbB***). Binding of EGF to the receptor leads to the induction of tyrosine kinase activity, and formation of dimers, as a result of which autophosphorylation occurs; stimulation of cell DNA synthesis and cell proliferation follows. Internalization of the EGF–receptor complex occurs subsequent to binding EGF. Example (precursor) from human: database code EGFR_HUMAN, 1210 amino acids (134.14 kDa).

epidermis the outermost layer of cells of an animal or plant. —**epidermal** *adj.*

epienzymatic control a form of control of arginine metabolism, occurring in some *Saccharomyces* spp., in which arginases bind stoichiometrically to ornithine carbamoyltransferase (EC 2.1.3.3), inhibiting the latter's activity but without substantially modifying the arginase activity. *See also* **epiprotein**.

epigenesis the concept that an organism develops from an originally undifferentiated mass of living material through the appearance of structures and functions not originally present.

epigenetic describing any of the mechanisms regulating the expression and interaction of genes, particularly during the development process. These include changes that influence the phenotype but have arisen as a result of mechanisms such as inherited patterns of DNA methylation rather than differences in gene sequence: **imprinting** is an example of this.

epigenetics the branch of biology dealing with the analysis of the mechanisms causing phenotypic effects to be produced by the genes of a genotype.

epiligrin an extracellular matrix protein, secreted by cultured epidermal keratinocytes. It is found in epithelial basement membranes but not membranes of endothelia, nor in muscle or nerve cells. It is a ligand for cell adhesion via **integrins**, with three chains linked by disulfide bonds, and is also an adhesive ligand for T lymphocytes. Example from the gene sequence of human epiligrin α3: database code HUMLAMAB, 145 amino acids (15.77 kDa). *See also* **laminin**.

Epilim *a proprietary name for* sodium valproate (*see* **valproic acid**).

epimer *(in stereochemistry)* either of two **diastereoisomers** that differ in configuration at only one chiral centre. The term includes **anomer**.

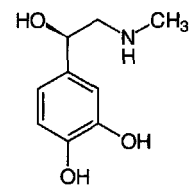
epimerase any enzyme within subclass EC 5.1, that catalyses **epimerization** (note that subclass EC 5.1 also includes **racemases**). Some epimerases, e.g. UDParabinose 4-epimerase (EC 5.1.3.5), contain tightly bound NAD, which undergoes oxidation and reduction during the reaction.

epimeric of or relating to an epimer or the chiral centre that specifies an epimer.

epimerization *or* **epimerisation** the process of converting an epimer into its diastereoisomer by altering the configuration at the epimeric chiral centre. —**epimerize** or **epimerise** *vb.*

epimino+ *an alternative term for* **imino+** (def. 2).

epinephrine *or* **adrenaline** (–)-1-(3,4-dihydroxyphenyl)-2-(methylamino)ethanol; a hormone secreted by the adrenal medulla and a neurotransmitter secreted by neurons in the brainstem. It is synthesized by the methylation of **norepinephrine**. It is an agonist for **adrenoceptors**, through which it has powerful glycogenolytic and lipolytic effects (both of which are mediated by cyclic AMP) and also affects the activity of smooth muscle (notably of the cardiovascular system and bronchi) and glandular tissue. Its mode of action critically depends on whether it acts through α or β adrenoceptors.The BP official name for this substance is Adrenaline; the USP official name for this substance is Epinephrine; Adrenalin is a USA trademark name. It was named adrenalin by Takamine in 1901.



epinephrine

epiphase the upper, less dense layer of a two-phase system. *Compare* **hypophase**. —**epiphasic** *adj.*

epiplasm a membrane skeleton of certain protists, that contributes to cell shape and patterning of the species-specific cortical architecture. This cytoskeleton contains proteins known as **articulins**.

epiprotein a specific protein, produced in certain circumstances in some *Saccharomyces cerevisiae* strains, that binds stoichiometrically to ornithine carbamoyltransferase (EC 2.1.3.3), thereby inhibiting its activity. It has subsequently been shown to have arginase activity and so is sometimes known as **epiarginase**. *See also* **epienzymatic control**.

episemantic molecule any molecule that is synthesized under the control of a tertiary **semantide**. All molecules built by enzymes in the absence of a template are included because, although they do not express extensively the information contained in the semantide, they are a product of this information. *See also* **asemantic molecule**.

episome **1** a genetic element that is sometimes found in cells, especially those of bacteria, and that can replicate either when integrated into or independently of the host chromosome. **2** any fragment of DNA that exists in a cell as an extrachromosomal element. This DNA may or may not be replicated and passed to daughter cells. The **plasmid** is an example of an episome. DNA elements that use transposases involved in phage lambda integration are also examples of episomes.

epithelium **1** *(in animal anatomy)* a sheet of closely packed cells, arranged in one or more layers, that covers the outer surfaces of the body or lines any internal cavity or tube (except the blood vessels, heart, and serous cavities). *Compare* **endothelium**, **mesothelium**. **2** *(in plant anatomy)* any of certain layers of parenchymal cells that line an internal cavity or tube. —**epithelial** *adj.*

epitope any immunological determinant group of an antigen. —**epitopic** *adj.*

epitype any class or group of related epitopes.

epoprostenol *international nonproprietary name for* prostaglandin I_2; *see* **prostacyclin**.

epothilone *see* **taxol**.

epoxidation the formation of an **epoxide** by addition of an oxygen atom as a bridge across the double bond of an alkene.

epoxide any compound where molecules contain an epoxy group attached to adjacent carbon atoms to form a saturated three-membered ring system.

epoxy+ *prefix (in chemical nomenclature)* indicating the presence in a molecule of an oxygen atom directly attached (by single covalent bonds) to two (adjacent or nonadjacent) carbon atoms of a carbon chain or ring system. Epoxy compounds are cyclic ethers.

epoxyeicosatrienoate *abbr.*: EpETrE *or (formerly)* EET; any of various metabolites of arachidonate that contain an epoxy group. They are formed by the action of cytochrome P450 – this occurs in numerous tissues and has a high degree of stereospecificity. The products are predominantly present esterified to membrane-bound phosphatidylcholine. They have a wide spectrum of biological activities, including stimulation of peptide hormone release, inhibition of Na^+,K^+-ATP-

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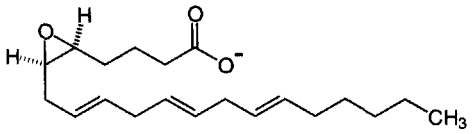
ase, mobilization of microsomal Ca^{2+}, and inhibition of prostaglandin-endoperoxide synthase. Examples are (all-*Z*)-5*S*,6*R*-epoxyeicosa-8,11,14-trien-1-oate and (all-*Z*)-11*S*,12*R*-epoxyeicosa-5,8,14-trien-1-oate. EpETrEs can be further metabolized to *vic*-diols, diepoxides, and other products.



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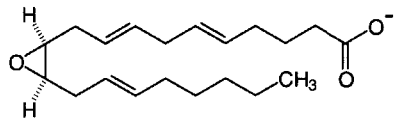


(all-*Z*)-11*S*,12*R*-epoxyeicosa-5,8,14-trien-1-oate

epoxy resin *or* **epoxide resin** any of a class of synthetic resins, containing ether linkages and epoxy groups, formed by the copolymerization of an epoxide (e.g. 1-chloro-2,3-epoxypropane) and a polyphenol (e.g. 2,2-bis(4-hydroxyphenyl)-propane). When mixed with certain accelerators, e.g. an amine or an anhydride, such resins produce hard, clear, resistant, thermosetting polymers that are used as adhesives and coatings and for embedding materials for microscopy, especially electron microscopy.

Eppendorf pipette any of a range of push-button, plunger-operated, precalibrated, dispensing micropipettes with disposable polypropylene tips. [After the name of the manufacturer.]

EPPS *an alternative name for* **Hepps**.

EPR *or* **epr** *abbr. for* electron paramagnetic resonance spectroscopy (*see* **electron spin resonance spectroscopy**).

epsilon *symbol*: ε (lower case) *or* E (upper case); the fifth letter of the Greek alphabet. For uses *see* **Appendix A**.

epsilon chain *or* **ε chain** the **heavy chain** of IgE **immunoglobulin** molecules.

EPSP *abbr. for* 5-*enol*pyruvylshikimate phosphate; an intermediate in aromatic amino-acid biosynthesis by the shikimate pathway (*see* **shikimate**).

EPSP synthase *an alternative name for* **3-phosphoshikimate 1-carboxyvinyltransferase**. *See also* **shikimate**.

Epstein–Barr virus human (gamma) herpesvirus 4; a DNA virus, first isolated from specimens of tumour tissue obtained from African children affected by Burkitt's lymphoma, that causes infectious mononucleosis (glandular fever) in young adult humans. [After (Sir) Michael Anthony Epstein (1921–), British pathologist and immunologist, and Yvonne M. Barr.]

eq. *or* **Eq.** *abbr. for* equivalent (def. 4).

equation of state any equation connecting the pressure, volume, and temperature of a substance or a mixture.

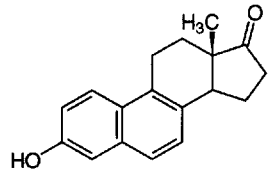
equatorial **1** of, relating to, or being an equator; located at or near an equator. *Compare* **axial** (def. 1). **2** *(in stereochemistry) symbol*: e; *see* **conformation**.

equi+ *comb. form* denoting equal or equality.

equi-effective dose ratio *abbr.*: EDR; the ratio of the doses of test and reference substances that produce the same biological effect (whether activation or inhibition).

equi-effective molarity ratio *abbr.*: EMR; the ratio of the molarity of test and reference substances that produce the same biological effect (whether activation or inhibition).

equilenin *the trivial name for* 3-hydroxyestra-1,3,5,7,9-pentaen-17-one; a weakly estrogenic steroid hormone isolated from the urine of pregnant mares. *Compare* **equilin**.



equilibrate to bring to equilibrium, or cause (something) to be in equilibrium (with some other thing), especially with the environment or with a (specified) system. —**equilibration** *n.*

equilibrium **1** a state of balance between or among opposing forces or processes that results in the absence of net change. **2** *(in chemistry)* a state of dynamic balance in a reversible chemical reaction when the reaction velocities in both directions are equal.

equilibrium assay a type of **radioimmunoassay** in which the reagents used are allowed to reach thermodynamic equilibrium. *Compare* **disequilibrium assay**.

equilibrium constant *symbol*: *K*; an expression of the position of the **equilibrium** (def. 2) of a reversible chemical reaction under specified physical conditions (e.g. temperature, pressure, nature of solvent, ionic strength, etc.). For a reaction of the generalized form:

$$aA + bB + \ldots \rightleftharpoons mM + nN + \ldots$$

when the thermodynamic **activity** of each of the components A, B, M, N, etc. is written as (A), (B), (M), (N), etc., and *a*, *b*, *m*, *n*, etc. are the respective numbers of molecular entities participating in the reaction, the equilibrium constant is given by:

$$K = [(M)^m(N)^n\ldots]/[(A)^a(B)^b\ldots]$$

Frequently in biochemical systems it is not possible to evaluate the activities of all the components; the **concentration equilibrium constant** (*symbol*: K_a) rather than the true or **thermodynamic equilibrium constant** is then calculated, *K* being expressed in terms of the molarities of each of the components in place of their activities. When the specified concentration of a component includes more than one chemical species (e.g. ionized plus un-ionized forms, or chelated plus unchelated metal ion) in unknown proportions, an **apparent (concentration) equilibrium constant** (*symbol*: *K′*) constrained with respect to certain variables (e.g. pH, or total concentration of metal ion), is written. *See also* **affinity constant**, **association constant**, **dissociation constant**, **p*K***.

equilibrium density-gradient centrifugation a method for the separation of cells, cell organelles, macromolecules, or other particles of different densities by centrifugation in a solution that increases in solute concentration, and hence in density, from the top to the bottom of the centrifuge tube. At equilibrium, particles of the same density are found as a band or zone in the density gradient. *Compare* **differential centrifugation**.

equilibrium dialysis a technique used to measure the binding of a **microsolute** or ions to a **macrosolute**. A solution of the macrosolute is placed inside a dialysis bag (through which the macromolecules will not pass); this represents phase α. The bag is suspended in a solution containing the microsolute (phase β). At equilibrium, any excess concentration of the microsolute in phase α is taken as evidence for binding. From a measurement of the excess concentration of the microsolute and knowledge of the concentration of the macrosolute the extent of the binding may be determined.

equilin *the trivial name for* 3-hydroxyestra-1,3,5(10),7-tetraen-17-one; a weakly estrogenic steroid hormone isolated from the urine of pregnant mares. *Compare* **equilenin**.

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equimolar of equal **molarity**.

equimolecular containing equal numbers of molecular entities.

equine of, relating to, or being a member of the family Equidae (horses, zebras, and asses); of, belonging to, characteristic of, obtained from, or relating to, a horse or horses; resembling a horse.

equiv. *abbr. for* equivalent (def. 3).

equivalence **1** the state of being equal, equivalent, or interchangeable. **2** **equivalency**. **3** the point or zone in a precipitin test at which antigen and antibody are present in optimal proportions for combination and precipitation.

equivalence factor *symbol* (for a chemical species X): $f_{eq}(X)$; a number pertaining to a given reacting component of a specified titrimetric reaction derived from consideration of the overall stoichiometry of the reaction. For a reaction of the following type: $\nu A + \nu B \rightarrow$ products, where νA and νB are the respective numbers of reacting entities, then the equivalence factor of species B is given by: $f_{eq}(B) = \nu B/\nu A$. When $\nu A > \nu B$ and $f_{eq}(A)$ is taken as unity, then $f_{eq}(B)$ is unity or less than unity. In the case of a reaction that can be clearly identified as acid–base or oxidation–reduction, the equivalence factor must be related to one entity of titratable hydrons or of transferable electrons, respectively.

equivalence point *or* **stoichiometric point** *or* **theoretical end point** the point in a titration at which the amount of titrant added is chemically equivalent to the amount of substance titrated.

equivalency *or* **equivalence** **1** the state of having equal valencies. **2** the state of having equal **equivalence factors**.

equivalent **1** equal or interchangeable in amount, importance, meaning, or value. **2** *(in chemistry)* having equal valencies. **3** something that is equivalent (to something else). **4** *(in chemistry)* **a** *abbr.*: equiv. *or* eq. *or* Eq.; a unit of amount of substance, defined as the entity of a chemical species that in a specified reaction would combine with, displace, or in any other appropriate way be equivalent to, one entity of titratable hydrons (in an acid–base reaction) or one entity of electrons (in an oxidation–reduction reaction). It is the arithmetic product of the **molar mass** of the chemical species and its **equivalence factor**. **b** *(formerly)* **equivalent weight**.

equivalent activity a measure of the radiation output of a real radiation source containing a particular radionuclide, defined as being equal to the **activity** (def. 1b) of a hypothetical point source of the same radionuclide that would give the same exposure rate at the same distance from the centre of the source. It is customarily used to express the strengths of most sources emitting high-energy gamma radiation.

equivalent ellipsoid of rotation the **ellipsoid of rotation** having the same volume as an actual hydrodynamic unit of a macromolecule in solution (which consists of the macromolecule and tightly bound solvent).

equivalent weight *abbr.*: equiv. wt.; an obsolete term defined as the weight in grams of an element, compound, or group that, in a specified reaction, will combine with or displace 8 grams of oxygen, or the equivalent weight of another chemical species. *See also* **equivalent** (def. 4).

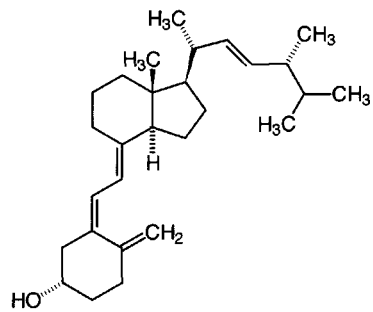
ER *abbr. for* endoplasmic reticulum.

erbA an oncogene (v-*erbA*) originally found in avian erythroblastosis virus; the corresponding protooncogene (c-*erbA*) encodes thyroid hormone receptor. Example, product of v-*erbA* from avian erythroblastosis virus: database code ERBA_AVIER, 385 amino acids (43.98 kDa); it requires the activity of other oncogenic agents for tumorigenesis. *See also* ***erbB***.

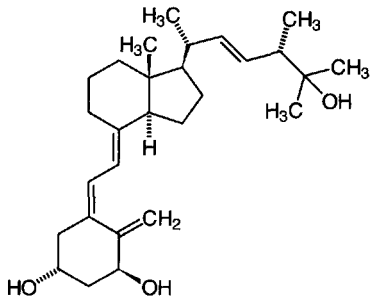
erbB an oncogene (v-*erbB*) from avian erythroblastosis virus; the corresponding protooncogene (c-*erbB*) encodes the **epidermal growth factor receptor**. In tumours the extracellular ligand-binding domain and the C terminus are deleted, contributing to a system with a constitutively active receptor protein. Example of protein product of v-*erbB* from avian erythroblastosis virus: database code ACBERBBH, 31 amino acids (3.50 kDa). The *erb* oncogene system is complicated; the transforming protein from the virus is a polyprotein product from *gag*, *erbA*, and *erbB*.

ercalcidiol *or (formerly)* **25-hydroxyergocalciferol** *the recommended trivial name for* (5*Z*,7*E*,22*E*)-(3*S*)-9,10(19),22-ergostatetraene-3,25-diol; a secosteroid with **vitamin D** activity. It is formed in the liver from **ercalciol** and converted to **ercalcitriol** in the kidney.

ercalciol *or* **ergocalciferol** *the recommended trivial name for* calciferol, vitamin D_2, (5*Z*,7*E*,22*E*)-(3*S*)-9,10-seco-5,7,10(19),22-ergostatetraen-3-ol; a secosteroid with **vitamin D** activity, obtained synthetically by UV-irradiation of **ergosterol**. It is the form of vitamin D most commonly used as a dietary supplement and for treatment of vitamin D deficiency. *International nonproprietary name*: ergocalciferol.



ercalcitriol *or (formerly)* **1α,25-dihydroxyergocalciferol** *the recommended trivial name for* (5*Z*,7*E*,22*E*)-(1*S*,3*R*)-9,10-seco-5,7,10(19),22-ergostatetraene-1,3,25-triol; a secosteroid with **vitamin D** activity. It is the biologically active metabolite of **ercalcidiol** and **ercalciol**.



ERE *abbr. for* estrogen response element (*see* **response element**).

erepsin a once-supposed single enzyme secreted by the mucosa of the small intestine and thought to be responsible for completing the breakdown in the gut of partially digested pro-teins into amino acids. It is now known to be a mixture of **peptidases**.

erg the cgs unit of work, defined as the work done by a force of 1 dyne acting over a distance of 1 cm; equivalent to 10^{-7} J.

ERG a gene encoding a family of transcription factors and related to the protooncogene *ETS*; it is named from '*ETS*-related gene'. It is expressed in some tumour-derived cell lines. Database code for expressed protein: ERG_HUMAN, 462 amino acids (52.03 kDa).

ergastoplasm *a term formerly applied to* the basophilic, fibrillar structures seen especially in pancreatic secretory cells; now termed rough **endoplasmic reticulum**.

+ergic *suffix (in pharmacology)* indicating agonist activity on a receptor in a neuron. *See*, e.g., **adrenergic**.

ergo+ *(comb. form)* **1** *or* (*before a vowel*) **erg+** denoting work. **2** *or* (*before a vowel*) **ergot+** denoting obtained from **ergot** or derived from a substance occurring naturally in ergot.

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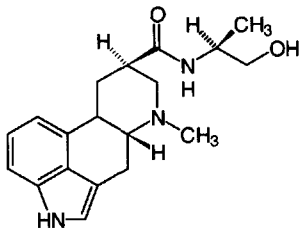
ergocalciferol *the alternative recommended trivial name and the international nonproprietary name for* **ercalciol**.

ergoflavin the major pigment from **ergot**.

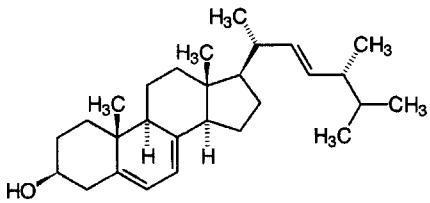
ergometrine *see* **ergonovine**.

ergonovine D-lysergic acid L-2-propanolamide; ergometrine; an **ergot alkaloid** noted for inducing sustained uterine contractions and used in the treatment of postpartum hemorrhage.



ergosome *(sometimes)* a **polyribosome**.

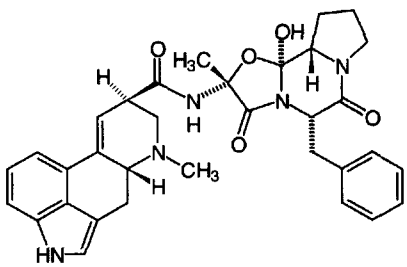
ergosterol *trivial name for* (22*E*)-ergosta-5,7,22-trien-3β-ol; (22*E*)-(24*R*)-24-methylcholesta-5,7,22-trien-3β-ol; a sterol found in ergot, yeast, and moulds. It is usually obtained industrially from yeast, which synthesizes it from simple sugars. It is the most important of the provitamins D. On irradiation with ultraviolet light it is converted to ercalciol (vitamin D_2).



ergot *the common name for* the sclerotial phase of the fungus *Claviceps purpurea*, which parasitizes the ovaries of cereals such as rye, and other grasses, leading to ergot-contaminated seeds. Ergot yields various medically useful alkaloids, including ergotamine and ergometrine, and is a source of lysergic acid. However, ingestion of contaminated seeds by livestock or humans can result in poisoning (**ergotism**).

ergot alkaloid any of a group of about 30 indole alkaloids obtainable from **ergot**. All are derivatives of **lysergamide** and are biosynthesized from L-tryptophan.

ergotamine 12′-hydroxy-2′-methyl-5′α-(phenylmethyl)ergotaman-3′,6′,18-trione; an **ergot alkaloid** with vasoconstrictor activity, used in the treatment of migraine.



ERIC *abbr. for* enterobacterial repetitive intergenic consensus sequence; any of a number of highly conserved partly palindromic sequences. They are reminiscent of **REPs** but are longer (120 bp) and are in extragenic sites.

ERK *abbr. for* from extracellular signal-regulated kinase; any of a sub-subclass (EC 2.7.–), protein kinases, also (more frequently) known as **MAP kinases**. Examples (all human): ERK1 (*or* insulin-stimulated MAP2 kinase) phosphorylates MAP2 and myelin basic protein; database code ERK1_HUMAN, 379 amino acids (43.09 kDa); ERK2 (*or* mitogen-activated protein kinase 2 *or* MAP kinase 2) is similar; database code ERK2_HUMAN, 360 amino acids (41.34 kDa); ERK3 (*or* MAP kinase isoform p63) has similar activity; database code ERK3_HUMAN, 557 amino acids (62.55 kDa).

ER mannosidase EC 3.2.1.–; *other name*: Man(9)-α-mannosidase; a glycoprotein enzyme of the *N*-glycosylation pathway of the endoplasmic reticulum that catalyses the removal of just one mannose residue from the core oligosaccharide of glycoproteins (Man(9)) to produce a specific isomer of Man(8)GlcNAc. Example (precursor) from human: database code MAN9_HUMAN, 625 amino acids (70.74 kDa). *See* **mannosidase**.

Ernst, Richard Robert (1933–) Swiss physical chemist noted for the application of pulsed radiofrequency radiation in nuclear magnetic resonance spectroscopy and the resultant extension of the technique to biological macromolecules; Nobel Laureate in Chemistry (1991) 'for his contributions to the development of the methodology of high resolution nuclear magnetic resonance (NMR) spectroscopy'.

erp60 *see* **calreticulin**.

ER-resident protein any protein that is retained by the endoplasmic reticulum. Their retention is regulated by the heterotetramer of a phosphoprotein (**calnexin**), a phosphoglycoprotein (*see* **Ssrα**), and two glycoproteins (*see* **Ssrβ**). *See also* **KDEL**.

'error catastrophe' hypothesis a hypothesis stating that since the protein synthetic machinery of the cell is itself made of protein, any imprecision in protein synthesis will lead to the formation of protein synthetic machinery of lowered accuracy, which will lead in turn to the production of even less precise machinery. If this positive feedback of error into the protein synthetic machinery is sufficiently high it will cause instability and an accelerating deterioration of the cell, resulting in cell death or loss of function.

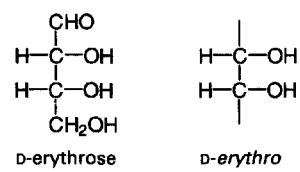
error-prone repair the processes of DNA repair, following damage, that give rise to 'fixed' mutations. Whether or not a particular damaged site will eventually lead to a mutation is dependent both on the genetic constitution of the cell and on environmental factors. It has been suggested that such mutations are due to errors in filling gaps in daughter DNA strands.

erucic acid *the trivial name for* (*Z*)-docos-13-enoic acid (22:1 *n*-9).

ERYF1 *see* **GATA-1**.

erythritol *i*-erythritol; *meso*-erythritol; *ms*-1,2,3,4-tetrahydroxybutane; *erythro*-1,2,3,4-butanetetrol; a polyol configurationally isomeric with (active) **threitol** but optically inactive through internal compensation. It occurs in certain fungi (where it appears to act as a storage carbohydrate), and is found also (as an ester of orsellinic acid) in some green algae and lichens. It is about twice as sweet as sucrose.

erythro- the configurational prefix to the systematic name of a polyhydric alcohol, especially of a monosaccharide, used to indicate the particular stereochemical configuration of a set of two contiguous CHOH groups that occurs in D- or L-erythrose; e.g. D-*erythro*-2-pentulose for D-ribulose. *Compare* ***threo-***.



D-erythrose D-*erythro*

erythro+ *or (before a vowel)* **erythr+** *or (sometimes)* **eryth+** *comb. form* **1** indicating red-coloured. **2** pertaining to red blood cells.

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erythroblast any of the nucleated red blood cells that are intermediates in the formation of a nonnucleated erythrocyte from a hemocytoblast. —**erythroblastic** *adj.*

erythrocruorin any of a group of respiratory pigments of invertebrates in the range of 0.4–6.7 MDa and containing 30–400 heme groups per molecule.

erythrocuprein *an alternative name for* **superoxide dismutase**.

erythrocyte a mature red blood cell; in mammals it is non-nucleated and lacks mitochondria. Erythrocytes contain, but are no longer capable of synthesizing, **hemoglobin** and they function in the transport of oxygen. Mammalian erythrocytes obtain energy from anaerobic glycolysis and also metabolize glucose via the phosphogluconate pathway. —**erythrocytic** *adj.*

erythrocyte sedimentation rate *abbr.*: ESR; the rate at which erythrocytes sediment as measured under defined conditions. An increased ESR is almost always indicative of organic disease and is associated with an increased concentration of fibrinogen, γ-globulin, α_2-macroglobulin, or γ_1-macroglobulin in the plasma.

erythrodextrin any of the larger **dextrins** that give a red colour with diiodine.

erythrogenesis *an alternative term for* **erythropoiesis**.

***erythro*-β-hydroxyaspartic acid** an amino acid formed by post-translational modification of an aspartyl residue at position 41 of the light chain of **protein C**.

erythroid **1** red or reddish in colour. **2** of or relating to **erythrocytes** or their precursors.

erythroid differentiation factor *see* **inhibin**.

erythrolabe a pigment that is sensitive to red light (570 nm) and is found in some retinal cones of the mammalian eye. It is lacking in subjects with red-blindness but is present in those with green-blindness. *Compare* **chlorolabe**, **cyanolabe**.

erythromycin any of several wide-spectrum macrolide antibiotics obtained from *Streptomyces erythreus*. Three components, A, B, and C, are produced during fermentation, the major component being erythromycin A. They inhibit protein synthesis in prokaryotes by binding to the 50S ribosomal subunit and inhibiting translocation.

erythromycin resistance factor any of several proteins that confer resistance to the antibiotic **erythromycin**. There are three mechanisms of resistance: (1) erythromycin esterase (EC 3.1.1.–), which is itself of two types (I and II); (2) a transmembrane export system (e.g. *erm* genes of *Arthrobacter* and certain Gram-positive bacteria); (3) rRNA (adenine-N^6-)-methyltransferase (EC 2.1.1.48), an enzyme that catalyses the reaction between *S*-adenosyl-L-methionine and rRNA to form *S*-adenosyl-L-homocysteine and rRNA containing N^6-methyladenine; example from *Staphylococcus aureus*: database code MLS2_STAAU, 244 amino acids (28.83 kDa); this protein produces a dimethylation of the adenine residue at position 2058 in 23S rRNA, resulting in reduced affinity between ribosomes and all macrolide, lincosamide, and streptogramin B-type antibiotics.

erythron *a collective term for* the circulating **erythrocytes** and their precursors.

erythrophore a type of chromatophore, coloured red and found especially in some fishes and crustaceans. The pigment, a carotenoid, is contained in bright red granules, which normally are dispersed throughout the cytoplasm, but which aggregate rapidly in response to epinephrine leading to near discoloration of the cell.

erythropoiesis *or* **erythrogenesis** the formation of red blood cells, in bone marrow or elsewhere. —**erythropoietic** *or* **erythrogenetic** *adj.*

erythropoietin a 46 kDa mammalian glycoprotein **cytokine**, formed in the kidneys and liver of mammals, that stimulates cellular differentiation of bone-marrow stem cells at an early stage of erythropoiesis, accelerates the proliferation and maturation of terminally differentiating cells into erythrocytes, and maintains a physiological level of circulating erythrocyte mass. The protein is now prepared from cDNA expressed in CHO cells and other cells. It is now established as the accepted treatment of chronic renal failure. Its receptor is a type I membrane protein. Examples (precursors, human): erythropoietin, database code EPO_HUMAN, 193 amino acids (21.28 kDa); erythropoietin receptor, database code EPOR_HUMAN, 508 amino acids (55.00 kDa).

erythrose *the trivial name for* the aldotetrose *erythro*-tetrose; it has D and L enantiomers, which are respectively diastereoisomeric with those of threose. *See* ***erythro-*** for structure.

erythrosome an artificial membrane preparation in which detergent-extracted, glutaraldehyde-fixed erythrocyte ghosts are coated with phospholipid.

erythrulose *the trivial name for* the ketotetrose *glycero*-tetrulose; it has D and L enantiomers.

ES *abbr. for* enzyme–substrate complex.

esc a regulatory gene in *Drosophila* that controls expression of ***BX-C*** genes in embryos. It is named from extra sex combs.

ESCA *abbr. for* electron spectroscopy for chemical analysis. *See* **photoelectron spectroscopy**.

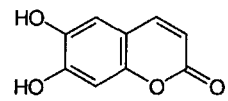
ES cell *abbr. for* embryonic stem cell.

Escherichia a genus of Gram-negative, rod-shaped, usually motile, chemoorganotrophic bacteria belonging to the family Enterobacteriaceae. It contains a single species, the colon bacillus, ***Escherichia coli***. [After Theodor Escherich (1857–1911), German physician, who (in 1885) isolated the colon bacillus and gave it its original name of *Bacterium coli commune*.]

Escherichia coli *or* **colon bacillus** *abbr.*: *E. coli*; the sole member of the bacterial genus *Escherichia* and arguably the most widely used experimental cell system in biochemistry and molecular biology. The cells are straight, round-ended rods, commonly 0.5–1 μm × 1–4 μm, and usually occurring singly or in pairs. The organism is present in the intestinal tract of humans and other animals and is common in soil and water. The numerous strains, some of which are enteropathogenic, are commonly distinguished serologically by their O, K, and H antigens. Strain O157 is a life-threatening enteropathogen with genes seemingly derived (at least in part) from *Shigella* spp. It produces both hemolysin and enterotoxin. *E. coli* takes part in bacterial conjugation and other forms of genetic transfer, and can be infected with some bacteriophages and plasmids. *See also* **toxin**.

Eschweiler–Clarke reaction *see* **reductive amination**.

esculetin 6,7-dihydroxycoumarin; an agent that selectively inhibits 5- and 12-lipoxygenase, without inhibiting prostaglandin-endoperoxide synthase.



E-selectin *see* **selectin**.

eserine *an alternative name for* **physostigmine**.

E-site the deacylated tRNA binding site in ribosomes; in bacteria this involves **ribosomal proteins** of the large subunit and 23S rRNA.

ESQL *abbr. for* embedded **SQL**; a computer language that allows SQL to interface with other programming languages, e.g. FORTRAN and **C**.

ESR *or* **esr** *abbr. for* **1** electron spin resonance. **2** erythrocyte sedimentation rate.

essential **1** of or being the essence of something; inherent. **2** absolutely necessary, basic, fundamental, indispensable, vitally important. **3** necessary for the normal growth of an organism but either not synthesized by that organism or synthesized at an inadequate rate. **4** *(in pathology)* describing a clinical condition or disorder that is not attributable to any discernible cause; **idiopathic** (def. 1). **5** relating to or derived from an extract of a plant, especially as an essence.

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essential amino acid any amino acid that cannot be synthesized by a cell or an organism in an amount corresponding to need. The extent to which a particular amino acid is essential in any one species of organism depends on the stage of development of the subject and its physiological state. The following L-amino acids are nutritionally essential for the maintenance of nitrogen equilibrium in an adult human: isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan, and valine. In addition, arginine and histidine are essential in growing children. The initial letters of the L-amino acids needed for optimal growth of infants or rats may be remembered using the mnemonic 'Many Very Hairy Little Pigs Live In The Torrid Argentine'. *Compare* **nonessential amino acid**.

essential fatty acid any polyunsaturated fatty acid that cannot be synthesized by a cell or an organism in an amount corresponding to need or from any dietary precursor. For mammals, linoleic acid (*see* **linoleate**) and (9,12,15)-linolenic acid (*formerly collectively known as* **vitamin F**) are nutritionally essential. *Compare* **nonessential fatty acid**.

essential fatty acid deficiency a condition that arises from the absence of **essential fatty acids** in the diet. A deficiency of fatty acids of the *n*-6 family (e.g. linoleic acid) in the diet of young animals results during growth in decreased body weight and, after some months, in increased skin permeability and capilliary fragility, and dermatitis. If prolonged into adulthood, poor litter sizes (e.g. in rats) and infertility can result. Deficiency of fatty acids of the *n*-3 family, in the presence of *n*-6 fatty acids, does not result in such obvious manifestations, partly because these fatty acids are tenaciously retained in tissues, and partly because *n*-6 fatty acids (e.g. 22:5 *n*-6) not normally present in significant amounts are synthesized and appear to compensate for the deficiency of *n*-3 fatty acids of similar length and degree of unsaturation. That the effects of deficiency are not solely due to lack of substrates for prostanoid synthesis is indicated by the ability of **columbinic acid** to relieve some of the effects.

essential fructosuria a relatively rare, hereditary, asymptomatic metabolic disorder characterized by the presence of fructose in the urine. In humans it is probably inherited as an autosomal recessive trait. Fructosuria occurs only after ingestion of fructose, which can also cause vomiting and aversion to sweet foodstuffs; long-term consequences can include failure to thrive, renal tubular dysfunction, and cirrhosis. Fructose metabolism involves formation of fructose 1-phosphate by ketohexokinase (EC 2.7.1.3); fructose 1-phosphate is then an (alternative) substrate for fructose-bisphosphate aldolase (EC 4.1.2.13) (I). Of the three isoenzymes of I (A, B, and C), B is much more active than A and C with fructose 1-phosphate as substrate. In essential fructosuria, the B isoenzyme of I is deficient and as a result there is a failure to metabolize fructose.

essential oil any of a group of volatile, odorous, natural oils obtained from plants. Such oils are usually benzene derivatives or **terpenes**, and are useful as flavouring agents or perfumes.

essential pentosuria *see* **pentosuria**.

EST *abbr. for* expressed sequence tag.

EST1 a gene involved in telomere maintenance, possibly coding for **telomerase**. It is named from 'even shorter telomeres'. It encodes a DNA-binding protein with RNA-directed DNA polymerase activity. Yeast gene product: database code EST1_YEAST, 699 amino acids (81.62 kDa).

established cell line cultured cells of a single origin that have the potential to be subcultured indefinitely whilst maintaining stable characteristics.

eSte *symbol for* the eleostearoyl group, CH_3–$[CH_2]_3$–$[CH{=}CH]_3$–$[CH_2]_7$–CO–.

ester any organic compound formed, either actually or formally, by the elimination of the elements of water between a hydroxyl group of an **oxoacid** (def. 1) and a hydroxyl group of either an alcohol or a phenol. Esters formed by condensation of one, two, or three molecular proportions of alcohol or phenol with one of a tribasic oxoacid may be termed monoesters, diesters, or triesters, respectively.

esterase any enzyme that catalyses the hydrolysis of an ester. Esterases form subclass EC 3.1 of the class EC 3, hydrolases, and are divided according to the nature of their substrates into the following sub-subclasses: EC 3.1.1, carboxylic ester hydrolases; EC 3.1.2, thiolester hydrolases; EC 3.1.3, phosphatases, phosphoric monoester hydrolases; EC 3.1.4, phosphodiesterases, phosphodiester hydrolases, phosphoric diester hydrolases (other than nucleases; see EC 3.1.11–3.1.31 below); EC 3.1.5; triphosphoric monoester hydrolases; EC 3.1.6, sulfatases, sulfuric ester hydrolases; EC 3.1.7, pyrophosphatases, diphosphoric monoester hydrolases; EC 3.1.8, phosphoric triester hydrolases; EC 3.1.11, exodeoxyribonucleases producing 5′-phosphomonoesters; EC 3.1.13, exoribonucleases producing 5′-phosphomonoesters; EC 3.1.14, exoribonucleases producing other than 5′-phosphomonoesters; EC 3.1.15, exonucleases active with either ribo- or deoxyribonucleic acids and producing 5′-phosphomonoesters; EC 3.1.16, exonucleases active with either ribo- or deoxyribonucleic acids and producing other than 5′-phosphomonoesters; EC 3.1.21, endodeoxyribonucleases producing 5′-phosphomonoesters; EC 3.1.22, endodeoxyribonucleases producing other than 5′-phosphomonoesters; EC 3.1.25, endodeoxyribonucleases specific for altered bases; EC 3.1.26, endoribonucleases producing 5′-phosphomonoesters; EC 3.1.27, endoribonucleases producing other than 5′-phosphomonoesters; EC 3.1.30, endonucleases active with either ribo- or deoxyribonucleic acids and producing 5′-phosphomonoesters; EC 3.1.31, endonucleases active with either ribo- or deoxyribonucleic acids and producing other than 5′-phosphomonoesters.

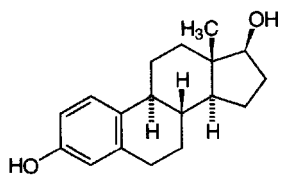
esteratic of, by means of, or having the activity of an esterase.

esterification the act or process of forming an ester from an oxoacid by condensing it with an alcohol or a phenol, or vice versa.

esterify to effect or to undergo esterification.

ester value *an alternative term for* **saponification number**.

17β-estradiol *or (esp. Brit.)* **17β-oestradiol** 1,3,5-estratriene-3,17β-diol; the most potent of the major **estrogens**. It is synthesized by the ovary, from which it is secreted directly into the circulation. Its formation depends on the presence of both **luteinizing hormone** and FSHRH; it is synthesized from testosterone by the aromatase complex, which is localized in ovarian granulosa cells, and is stimulated by follitropin; lutropin, on the other hand, stimulates production of testosterone, the aromatase substrate, by ovarian thecal cells. Apart from being important during development in inducing female characteristics, 17β-estradiol is important during the first half of the menstrual cycle (i.e. before ovulation) in stimulating proliferation of the epithelial and stromal layers of the endometrium in preparation for ovulation; it also stimulates production by the liver of proteins that bind steroids and thyroxine. During pregnancy, synthesis of estrogens is greatly increased, most of this increase being due to synthesis by the fetal adrenal gland of the precursors dehydroepiandrosterone and 16-hydroxydehydroepiandrosterone.



estramustine *or (esp. Brit.)* **oestramustine** estradiol 3-bis(2-chloroethyl)carbamate; an ester formed between estradiol and

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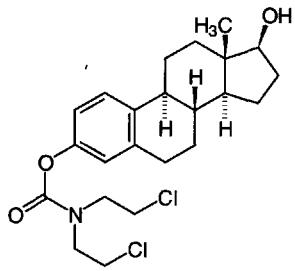
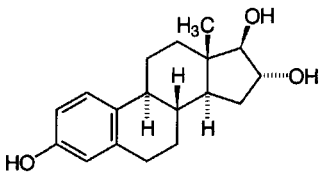
the carbonic-acid analogue of nitrogen mustard (mustine); it has antineoplastic activity.

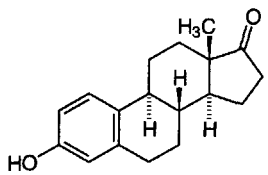


estriol *or (esp. Brit.)* **oestriol** 16α-estradiol; 1,3,5-estratriene-3,16α,17β-triol; a relatively weak estrogen produced mainly during pregnancy. It is synthesized by the placenta from 16α-hydroxydehydroepiandrosterone sulfate, which is formed in fetal liver from dehydroepiandrosterone sulfate secreted by the fetal adrenal gland. Urinary estriol is measured to monitor fetal well-being in high-risk pregnancies. Low levels are also associated with the inherited X-linked disorder, placental sulfatase deficiency.



estrogen *or (esp. Brit.)* **oestrogen** any substance, natural or synthetic, that produces changes in the female sexual organs similar to those produced by 17β-estradiol, the principal hormone of the vertebrate ovary. Naturally occurring estrogens are C_{18}-steroid hormones; they are produced also by the placenta, adrenal cortex, and testis, as well as by many species of plants. *Compare* **androgen**. —**estrogenic** *or* **oestrogenic** *adj.*

estrone *or (esp. Brit.)* **oestrone** 1,3,5-estratrien-3-ol-17-one; a major estrogen, also called folliculin, synthesized and secreted by the ovary, in which it is formed from androstenedione by the aromatase complex. However, estrone is mainly synthesized in peripheral tissues, from androstenedione taken up from the circulation. Its actions are similar to those of **17β-estradiol**.



estrone sulfotransferase EC 2.8.2.4; an enzyme involved in the inactivation of estrogens. It catalyses the reaction of 3′-phosphoadenylylsulfate with estrone to form the inactive estrone 3-sulfate with release of adenosine 3′,5′-bisphosphate. Example from *Bos taurus*: SUOE_BOVIN, 295 amino acids (34.60 kDa).

estrophile *(sometimes)* estrogen receptor.

estrous cycle *or (esp. Brit.)* **oestrous cycle** the hormonally controlled cycle of activity of the reproductive organs of non-pregnant, sexually mature females of many species of mammal. It may be continuous or seasonal, depending on species. There are four principal phases. (1) **Follicular phase** *or* **estrus** – ovarian Graafian follicles mature, estrogen secretion by the ovary is at its highest, and the endometrium proliferates; the phase culminates in ovulation; in seasonal animals it is the time of sexual receptivity. (2) **Luteal phase** *or* **metestrus** – the corpus luteum develops in the ovary, estrogen secretion diminishes, and progesterone secretion reaches its maximum. (3) **Diestrus** – the corpus luteum and endometrium regress, new follicular growth begins, and progesterone secretion diminishes. (4) **Proestrus** – the corpora lutea involute, Graafian follicles re-emerge, and gonadal hormone secretion is at its lowest. The cycle then recommences.

estrus *or (esp. Brit.)* **oestrus** the first phase of the **estrous cycle**. —**estrous** *or (esp. Brit.)* **oestrous** *adj.*

esu *or* **ESU** *abbr. for* electrostatic unit.

Et *symbol for* the ethyl group, CH_3–CH_2–.

ET *abbr. for* endothelin.

eta **1** *symbol*: η (lower case) *or* H (upper case); the seventh letter of the Greek alphabet. For uses *see* **Appendix A**. **2** *(in chemical nomenclature) a less common alternative name for* **hapto**.

ETF *abbr. for* electron-transfer flavoprotein *or* electron-transferring flavoprotein.

ethambutol (+)-*N*,*N*′-bis(1-hydroxymethylpropyl)ethylenediamine; an antitubercular drug.

ethanol *or (formerly)* **ethyl alcohol** CH_3–CH_2–OH; a colourless, water-miscible, flammable liquid. It is produced by **alcoholic fermentation** and is thereby probably the single most important product of bioindustry in economic terms. However, most ethanol (not destined for human consumption) is now manufactured from ethylene as a by-product in the petroleum industry. Commonly known as alcohol.

ethanolamine-phosphate cytidylyltransferase EC 2.7.7.14; *other name*: phosphorylethanolamine transferase; an enzyme that catalyses the reaction of CTP and ethanolamine phosphate to form **CDPethanolamine** with release of pyrophosphate.

ethanolaminephosphotransferase EC 2.7.8.1; an enzyme of the pathway for *de novo* synthesis of phosphatidylethanolamines. It catalyses the reaction of CDPethanolamine with 1,2-diacylglycerol to form phosphatidylethanolamine with release of CMP. Example from yeast: database code EPT1_YEAST, 391 amino acids (44.51 kDa). *Compare* **phosphatidylserine decarboxylase**.

ethanol fermentation *an alternative term for* **alcohol fermentation**.

ethanolic of, containing, or derived from ethanol; dissolved in pure or aqueous ethanol.

ethanolysed cellulose a powdered and highly purified form of cellulose, formerly in use as a supporting medium in preparative zone electrophoresis of proteins, e.g. serum proteins. It is prepared by heating fibrous cotton (cotton wool) under reflux for approximately 24 h with acid-ethanol (absolute ethanol made 1 molar with respect to HCl either by introduction of dry hydrogen chloride gas or by reaction with acetyl chloride). By this means, partial alcoholysis of the cellulose occurs and acidic groups are neutralized by esterification, the cotton fibres being partially degraded into nonclumping particles; at the same time, light-absorbing and other interfering impurities are extracted from the cellulose.

ether **1** any anhydride, of general formula R^1–O–R^2, formed between two (identical or nonidentical) organic hydroxy compounds. **2** *the common name for* **diethyl ether** (*or* ethyl ether *or* ethoxyethane), C_2H_5–O–C_2H_5.

ethereal *(in chemistry)* of, containing, or dissolved in an ether, especially diethyl ether.

ethereal sulfate *an obsolete term for* any biogenic half-ester of sulfuric acid with an aromatic hydroxy compound. Ethereal sulfates are found in the urine as end products of sulfur metabolism and metabolism of some aromatic compounds.

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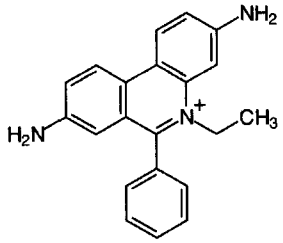
ether lipid any lipid that contains (normally) one fatty alcohol in ether linkage to one of the carbon atoms (normally C-1) of glycerol. They are found in low concentrations in glycerophospholipid fractions, the constituent at C-2 of the glycerol moiety then being an acyl group. **Platelet-activating factor** is an important physiologically active ether glycerophospholipid. Ether linkages in neutral acylglycerols are known, and contain one fatty alcohol linked to glycerol by an ether linkage (usually at C-1), with fatty acids in ester linkage at the other two positions. The ether linkage resists hydrolysis, and typical hydrolysis products are the glyceryl ethers such as **batyl alcohol**, **chimyl alcohol**, and **selachyl alcohol**.

ethidium the 3,8-diamino-5-ethyl-6-phenylphenanthridinium cation, usually used as the bromide salt. It binds by **intercalation** to double-stranded regions of DNA and RNA molecules with marked enhancement of fluorescence. It is used as a trypanocide and to reveal double-stranded DNA and RNA in gel electrophoresis.



ethinylestradiol *the international nonproprietary name for* ethynylestradiol; 17α-ethynyl-1,3,5(10)-estratriene-3,17β-diol]; (17α)-19-norpregna-1,3,5(10)-trien-20-yne-3,17-diol; a synthetic steroid with potent estrogenic activity, commonly used in oral contraceptive preparations.

ethionine *S*-ethyl-L-homocysteine; a synthetic, carcinogenic analogue of methionine. Its toxicity is due to the fact that it competes with methionine for the enzyme **methionine adenosyltransferase**, with the result that *S*-adenosylmethionine is formed. This leads to a deficiency of ATP.

ethoxy *symbol*: OEt *or* Eto; the alkoxy group, CH_3–CH_2–O–, derived from ethanol by loss of a hydrogen atom.

ethyl *symbol*: Et; the CH_3–CH_2– alkyl group, derived from ethane.

ethyl alcohol *the former name for* **ethanol**.

ethylene CH_2=CH_2; a colourless gas and the first member of the olefin (or alkene) series of hydrocarbons. It occurs naturally as a phytohormone, with a number of physiological effects, the most important being stimulation of ripening of fleshy fruit and stimulation of abscission of leaves. *See also* **ethylene-forming enzyme**.

ethylenediaminetetraacetate *see* **EDTA**.

ethylene-forming enzyme *abbr.*: EFE; *other name*: 1-aminocyclopropane-1-carboxylate (ACC) oxidase. An enzyme component of the biosynthetic pathway for the formation of the plant hormone **ethylene**; it catalyses a reaction between 1-aminocyclopropane-1-carboxylate and O_2 to form ethylene, HCN, CO_2, and two molecules of $2H_2O$; iron and ascorbate are cofactors. The enzyme is a **dioxygenase** but structurally unrelated to other examples of these. Example from tomato: database code ACC1_LYCES, 316 amino acids (35.93 kDa).

ethylenic containing one or more aliphatic carbon–carbon double bonds, as in **ethylene**.

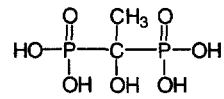
***N*-ethylmaleimide** *abbr.*: NEM; an agent that reacts irreversibly with thiol groups in proteins; it is useful as an inhibitor in transport studies and of thiol enzymes.

***N*-ethylmaleimide-sensitive fusion protein** *abbr.*: NSF protein; a homotetrameric cytoplasmic protein required for vesicle-mediated transport and transport from the endoplasmic reticulum to the Golgi stack. Example from Chinese hamster: database code SC18_CRIGR, 744 amino acids (82.44 kDa). *See also* **SNAP** (def. 3).

ethynylestradiol *see* **ethinylestradiol**.

ETI *see* **eicosatriynoic acid**.

etidronate any anion of etidronic acid, (1-hydroxyethylidene)bisphosphonic acid, an analogue of diphosphoric acid in which the latter's bridging oxy group is replaced by a 1-hydroxyethylidene group. Disodium etidronate is useful clinically for reducing the turnover rate of bone, e.g. in osteoporosis or in Paget's disease of bone.



etidronic acid

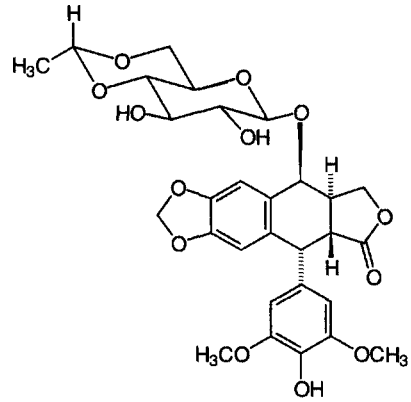
etiology *or (esp. Brit.)* **aetiology** the cause or causes of disease and their study.

Etn *symbol for* a residue of ethanolamine, H_2N–CH_2–CH_2–O–.

EtO *or* **OEt** *symbol for* the ethoxy group, CH_3–CH_2–O–.

ES cell *abbr. for* embryo-derived stem cell.

Etoposide a semisynthetic lignan derivative prepared from **podophyllotoxin**. It is useful as an antitumour agent in multidrug therapies, exerting its effect probably through interaction with topoisomerase II, which it inhibits; it also inhibits nucleoside transport in mammalian cells.



ETS *abbr. for* expression tagged site; a jargon phrase from genome mapping projects, etc. meaning a DNA database code (usually short) corresponding to an actively transcribed gene (i.e. cDNA from mRNA) of known sequence but, in general, of unknown function. Large ETS libraries are used in the Human Genome Project and similar projects on other organisms.

ETS a protooncogene related to v-*ets*, one of the oncogenes of the acutely transforming avian erythroblastosis virus E26; is named from 'E twenty-six specific'. It encodes a family of transcription factors: Ets1 activates stromelysin and collagenase genes and binds to the enhancer sequence of the TCRα gene; it is expressed in tumours of the peripheral nervous system and in Ewing's sarcoma; Ets1 and Ets2 are kinase substrates. Example of expressed protein: database code ETS1_HUMAN, 441 amino acids (50.41 kDa).

ETYA 5,8,11,14-eicosatetraynoic acid (*see* **eicosatetraynoic acid**).

eu+ *prefix* **1** indicating well, pleasant, good. **2** indicating normal, true, typical. In medicine, sometimes used interchangeably with **normo+**.

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e.u. *symbol for* entropy unit.
Eu *symbol for* europium.
EU *abbr. for* enzyme unit (obsolete).
Eubacteria *a name suggested for* one of three major lineages of cellular organisms, the others then being **Archaebacteria** and **eukaryotes**, defined when organisms are classified on the basis of sequence homologies of their ribosomal RNA. It comprised all typical bacteria, the major subdivisions being the cyanobacteria, the Gram-positive bacteria, and the Gram-negative bacteria. This classification has now been superseded: *see* **Archaea**, **Bacteria**, and **Eukarya**.
eucaryon *a variant spelling of* **eukaryon**.
eucell any cell of a **eukaryote**.
euchromatin the dispersed less dense form of **chromatin** in the interphase **nucleus**. It exists in at least two forms, about 10 per cent being in the form of transcriptionally active chromatin which is the least condensed, while the rest is inactive euchromatin which is more condensed than active chromatin but less condensed than **heterochromatin** which represents about 10 per cent of the chromatin in the interphase nucleus.
eucollagen **1** a highly modified form of **collagen** that can be easily and completely transformed into gelatin. **2** a hypothetical limiting structure for collagen in which Gly occurs at intervals of three residues and Hyp at intervals of ten residues; it is considered to be responsible for the 28.6 repeat distance in the X-ray diffraction pattern.
eugenics *(functioning as sing.)* the study of methods of improving the hereditary characters of the human race, especially by selective breeding. —**eugenic** *adj.*
Euglena a genus of fusiform, photosynthetic protozoa (sometimes classified as algae) of the division Euglenophyta. They are useful in biochemical research as unicellular photosynthetic organisms.
euglobulin any 'true' globulin of blood plasma that is soluble in isotonic salt solutions, insoluble at low ionic strengths (or in pure water), and precipitated by addition of saturated ammonium sulfate solution to a final concentration of 33%. *Compare* **pseudoglobulin**.
euglycemia *or* **normoglycemia** the condition or state in which the blood glucose level is within the normal range. *See also* **glycemia**. —**euglycemic** *adj.*
Eukarya one of the three major kingdoms of cellular organisms, the others being Archaea and Bacteria. The eukarya are characterized by the presence of a **eukaryon**.
eukaryon *or (sometimes)* **eucaryon** (*pl.* **eukarya** *or* **eucarya**) the type of cell nucleus bounded by a nuclear membrane and containing true chromosomes. It is characteristic of all multicellular and unicellular organisms except bacteria, actinomycetes, and cyanobacteria. *Compare* **prokaryon**.—**eukaryous** *or* **eucaryous** *adj.*
eukaryosis *or (sometimes)* **eucaryosis** the condition of possessing a **eukaryon**. —**eukaryotic** *or* **eucaryotic** *adj.*
eukaryote *or (sometimes)* **eucaryote** any organism whose cells contain a **eukaryon** (or eukarya) and undergo meiosis. *Compare* **prokaryote**.
eukaryotic porin *see* **porin**.
Euler **1 Hans Karl August Simon von Euler-Chelpin** (1873–1964), father of U.S. von Euler (*see* **von Euler** (def. 2)) and generally known as Hans von Euler or Euler, German-born Swedish chemist and biochemist distinguished for his work on the enzymic mechanism of fermentation and in particular for his isolation, naming, and study of the chemical nature and functions of cozymase (now known as NAD); Nobel Laureate in Chemistry (1929), the prize being shared with A. Harden 'for their investigations on the fermentation of sugar and fermentative enzymes'. **2 Ulf Svante von Euler** *see* **von Euler** (def. 2).
Euler-Chelpin *see* **Euler** (def. 1).
eumelanins *see* **melanin**.
eupeptide *a name suggested for* any physiologically active gastrointestinal polypeptide.
eupeptide bond *a name suggested for* a peptide bond formed specifically between C-1 of one amino-acid residue and N-2 of another residue. *Compare* **isopeptide bond**.
euploid having a chromosome number that is an exact multiple of the monoploid number; i.e. each chromosome of the set is present in the same number. *Compare* **aneuploid**. —**euploidy** *n.*
euthyroid having a normally functioning thyroid gland and normal levels of thyroid hormones.
eutopic binding *(sometimes) an alternative term for* **productive binding**.
eutrophic describing a habitat, esp. a lake or other mass of water, that contains abundant nutrients, both organic and inorganic, and hence favours excessive growth of aerobic plants and microorganisms. Such growth results in depletion of dissolved dioxygen and, ultimately, extinction of aerobic life. *Compare* **dystrophic** (def. 2), **oligotrophic**.
eutrophication the process of becoming or rendering eutrophic.
eV *symbol for* electronvolt.
event marker a feature of some chart recorders by means of which a mark is made on the chart to record the occurrence of a specifiable event or series of events, e.g. the stepwise operation of a fraction-collecting device.
evolution **1** *(in biology)* the process of cumulative change occurring in the form and mode of existence of a population of organisms in the course of successive generations related by descent. **2** *(in chemistry)* the liberation of a gas, or of heat, in the course of a chemical reaction. —**evolutionary** *or* **evolutional** *adj.*
evolve **1** to develop gradually; to cause to develop. **2** *(in biology)* to undergo **evolution** (def. 1). **3** *(in chemistry)* to give off a gas or heat.
ex+ **1** *prefix* indicating out of, away from, outside of; without, lacking; former. **2** *comb. form* a variant of **exo+** *(sometimes before a vowel)*.
exa *symbol*: E; the SI prefix denoting 10^{18} times.
EXAFS *abbr. for* extended X-ray absorption fine structure (spectroscopy).
excelsin a crystallizable globulin of ≈290 kDa obtained from the seed of the brazil-nut tree, *Bertholettia excelsa*. It structurally resembles arechin, edestin, and glycinin.
exchange **1** to cause two different objects to change places with each other. **2** the act or process of exchanging. **3** *(in genetics)* the reciprocal exchange of chromatid segments between chromosomes at meiosis or mitosis that results in genetic recombination.
exchange diffusion the exchange of ions or molecules across a (biological) membrane; it can be by simple diffusion or be carrier-mediated.
exchange labelling the catalysed exchange of one nuclide for another radioactive or stable nuclide of the same element in a chemical compound in order to produce an isotopically labelled form. The procedure is useful esp. in the preparation of tritium-labelled compounds.
exchanger a substance upon which, or a device by which, an **exchange** (def. 2) can be effected; e.g. an ion exchanger, or a heat exchanger.
exchange reaction a chemical reaction that results in the production of a substance that is chemically identical with the starting material. It is not detectable by traditional chemical analysis but (often) is demonstrable with the help of (radio)isotopes.
excimer an adduct formed between a molecular entity that has been excited by a photon and an identical unexcited molecular entity; the adduct exists until it fluoresces by emission of a photon. An excimer is recognized by the production of a new fluorescent band at a longer wavelength than that of the usual emission spectrum. Its formation is distinguishable from resonance energy transfer in that the excitation spectrum is identical with that of the monomer.

excitation: $A + photon \rightarrow A^*$
excimer formation: $A^* + A \rightarrow D^*$
excimer fluorescence: $D^* \rightarrow A + A + photon$

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excinuclease a DNA-repair endonuclease. An example is the ABC excision nuclease of *Escherichia coli*; this comprises three subunits, named from the corresponding ***uvr*** genes. UvrA is an ATPase and DNA-binding protein that preferentially binds single-stranded or UV-irradiated double-stranded DNA; it belongs to the **ABC transporter** family; database code UVRA_ECOLI, 940 amino acids (103.75 kDa). UvrB stimulates the activities of UvrA; database code UVRB_ECOLI, 673 amino acids (76.14 kDa). UvrC is a nuclease component; database code UVRC_ECOLI, 588 amino acids (65.64 kDa).

excisase an enzyme involved in lambda phage induction. *See* **integrase**.

excise to cut out or remove, as of a tumour, organ, or part of a linear polymer.

excision **1** the act or process of excising, especially the enzymic removal of an oligonucleotide segment from a nucleic-acid molecule. **2** *(in genetics)* the separation of one or more replicons from a cointegrate.

excisionase *see* **Xis protein**.

excision repair one of the intracellular mechanisms for the repair of DNA lesions (single-strand breaks, damaged bases, etc.). It occurs in the following stages: (1) recognition of the damaged region; (2) removal of the damaged oligonucleotide by two enzymic nucleolytic reactions (excision); (3) synthesis by DNA polymerase of the excised oligonucleotide using the second (intact) DNA strand as template; and (4) covalent joining by DNA ligase of the newly synthesized segment to the existing ends of the originally damaged DNA strand. The process is light-independent. *Compare* **photoreactivation**, **post-replication repair**. *See also* **short-patch repair**.

excitability proteins *a collective name for* intrinsic membrane proteins that are ion channels, receptors, and ion pumps.

excitable capable of responding to a stimulus; used especially of a biological membrane, neuron, or other living matter. —**excitability** *n.*

excitable membrane any biological membrane capable of responding to a specific chemical or physical stimulus. Such membranes are commonly characterized by: (1) the presence of a highly specific, integral protein receptor; (2) the occurrence of a conformational change in the receptor in response to the specific stimulus with a consequential change in membrane permeability or in the activity of a membrane-bound enzyme; and (3) reversibility of the alterations in conformation of the receptor and functional activity of the membrane.

excitation–contraction coupling a general term often used to refer to the coupling of an excitatory stimulus to the contraction of muscle; the process by which the fibres of a muscle are caused to contract by the stimulation of a neuron.

excitation spectrum any **spectrum** of electromagnetic radiation that, when applied to a sample, causes the atoms and molecules of the sample to become excited by the absorption of energy and, when reverting to their normal energy levels, to emit radiation of different frequencies to that of the absorbed radiation. *Compare* **absorption spectrum**, **emission spectrum**.

excitatory able to excite; stimulatory.

excitatory amino-acid receptor a receptor for any excitatory amino-acid in the central nervous system. These comprise two main groups: ionotropic, regulating an intrinsic ion channel, or metabotropic, coupled to either the cAMP or inositol phospholipid second messenger systems. The three main types of ionotropic receptors all have four transmembrane domains and are characterized pharmacologically by selective agonists: *N*-methyl-D-aspartate (NMDA), α-amino-3-hydroxy-5-methylisoxazole (AMPA), and kainate. NMDA receptors have a further binding site for glycine, which modulates receptor activation. All such ionotropic receptors regulate Na^+ and K^+ conductance; NMDA receptors additionally regulate Ca^{2+} conductance. Seven subtypes of **metabotropic** receptor have been cloned, all with seven transmembrane domains (mGlu1 to mGlu7): mGlu1 and mGlu5 modulate inositol phospholipid turnover while mGlu2, mGlu3, mGlu4, mGlu6, and mGlu7 are all negatively coupled to adenylate cyclase.

excite **1** to raise a molecular entity from its ground state to an excited state by the input of energy. **2** to cause an increase in activity or other response in an organism or part of an organism. —**excitation** *n.*

excited state any state of a molecular entity that has a higher energy level than its ground state.

exciter any device that excites, or raises a substance to an excited state.

exciton any nonconducting nonlocalized neutral entity that occurs in semicrystalline semiconductors, consisting of an excited electron bound to a positive hole, the combination forming a concentration of energy with certain properties characteristic of a particle.

exciton splitting the splitting of electronic absorption bands of a population of identical chromophores that are arranged in space such that sets of two or more are in close proximity. The splitting arises from electronic interactions between excited and nonexcited chromophores within the sets.

exclusion chromatography *an alternative name for* **permeation chromatography**.

exclusion limit an attribute of a specific gel used in **gel-permeation chromatography**. It is the relative molecular mass of the largest molecule of a particular shape that can be effectively fractionated by its use.

exclusion principle *see* **Pauli exclusion principle**.

exclusion reaction the reaction of a phage-infected bacterium that prevents the entry of additional phages. It is brought about by the strengthening of the bacterial cell envelope.

exclusion volume the volume of solvent retained by the column bed in **gel-permeation chromatography** that is outside the gel particles. *Compare* **void volume**.

excrete to eliminate waste materials (from a body or organism). —**excretion** *n.*; **excretive** *or* **excretory** *adj.*

exendin any of several peptides belonging to the glucagon family that have been isolated from *Heloderma* spp., exendin-1 (*or* **helospectin I**), exendin-2 (*or* **helodermin**) and exendin-4 from *Heloderma suspectus* and exendin-3 from *Heloderma horridus horridus*. They have biological activity similar to vasoactive intestinal peptide and secretin. Exendin-4 shares 53 per cent similarity in its primary structure with glucagon-like peptide 1 (GLP-1) (7–36) amide. The latter binds to exendin receptors on pancreatic acinar cells, and exendin (9–39) (from exendin-3 or -4) is a GLP-1 receptor antagonist which blocks the inhibitory effect of GLP-1 on food intake of fasted rats. Exendin-4 is

HGEGTFTSDLSKQMEEEAVRLFI-
EWLKNGGPSSGAPPPS

(database code EXE4_HELSU, 4.188 kDa); exendin-3 is similar except for residues 1–3 which are HSD.

exergonic describing any process or reaction that can produce work; i.e. one that, at constant pressure and temperature, results in a negative change in free energy content. *Compare* **endergonic**.

exhaustive methylation the maximal methylation of all groups in a substance that are capable of being methylated; it is useful in structural studies of carbohydrates, alkaloids, etc.

exo+ *or (sometimes before a vowel)* **ex+** *comb. form* indicating outside, external, outer. *Compare* **endo+**. *See also* **exo-**.

exo- *prefix (in stereochemistry) see* **conformation**.

exocellular describing cellular components that are external to the cell membrane but attached to its outer surface. *Compare* **extracellular**.

exocrine **1** describing or relating to a gland or other group of cells that discharges its secretion through a duct. **2** relating to a secretion of exocrine tissue. **3** a product of exocrine tissue. *Compare* **endocrine**.

exocytic **1** situated outside a living cell and not belonging to

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the cell itself; extracellular. **2** *an alternative term for* exocytotic (*see* **exocytosis**).

exocytose to effect exocytosis. —**exocytosed** *adj.*

exocytosis the discharge by a cell of intracellular materials to the exterior by **emiocytosis** or reverse **pinocytosis**. *Compare* **endocytosis**, **transcytosis**. *See also* **externalize**. —**exocytic** *or* **exocytotic** *adj.*

exodeoxyribonuclease *see* **deoxyribonuclease**.

exodeoxyribonuclease I EC 3.1.11.1; *other names*: exonuclease I; *Escherichia coli* exonuclease I. An enzyme that catalyses exonucleolytic cleavage of DNA in the 3′- to 5′- direction, releasing 5′-phosphomononucleotides. It shows a preference for single-stranded DNA. Database code EX1_ECOLI, 475 amino acids (54.44 kDa).

exodeoxyribonuclease V EC 3.1.11.5; *other names*: exonuclease V; *Escherichia coli* exonuclease V; RecBC. An enzyme that catalyses exonucleolytic cleavage of DNA (in the presence of ATP), in either the 5′- to 3′- or the 3′- to 5′-direction, to yield 5′-phosphooligonucleotides. Database codes of the subunits (products of genes *recA*, *recB*, and *recC*): RecA: EX5A_ECOLI, 608 amino acids (66.89 kDa); RecB: EX5B_ECOLI, 1180 amino acids (133.81 kDa); RecC: EX5C_ECOLI, 1122 amino acids (128.70 kDa).

exodeoxyribonuclease VII EC 3.1.11.6; *other names*: exonuclease VII; *Escherichia coli* exonuclease VII. An enzyme that catalyses exonucleolytic cleavage of DNA, in either the 5′- to 3′- or the 3′- to 5′-direction, to yield 5′-phosphomononucleotides.

exodeoxyribonuclease (phage SP3-induced) EC 3.1.11.4; *other names*: phage SP3 DNase; DNA 5′-dinucleotidohydrolase. An enzyme that catalyses exonucleolytic cleavage of DNA in the 5′- to 3′-direction to yield 5′-phosphodinucleotides.

exoenzyme **1** any enzyme that occurs attached to the outer surface of a cell (i.e. an **ectoenzyme**) or in the periplasmic space, or one that is secreted by a cell into the medium. *Compare* **endoenzyme** (def. 1). **2** any enzyme that cleaves a linkage to the terminal residue of a biopolymer. *Compare* **endoenzyme** (def. 2).

exogenous originating outside an organism, tissue, or cell, e.g. nutrients; of or pertaining to external factors that affect an organism, e.g. light. —**exogenously** *adv.*

exomorphin *see* **casomorphin**.

exon **1** any coding or messenger sequence of deoxynucleotides; i.e. any intragenic region of DNA in eukaryotes that will be ultimately expressed in (mature) mRNA or rRNA residues. An arrangement of exons alternating with **introns** constitutes a **transcriptional unit**. **2** ordinary title of any of the four most junior officers of the Yeomen of the Guard (Beefeaters, Warders of the Tower of London, appointed by the monarch) who in turn act as resident commanders in the absence of superior officers. —**exonic** *adj.*

exon shuffling the recombination of different coding regions of eukaryotic structural genes (i.e. **exons**) through crossing-over, a mechanism proposed to explain the mosaic structure of eukaryotic genes. Such a mechanism is also responsible for the generation of, e.g., antibody diversity.

exonuclease any enzyme of a group of phosphoric diester hydrolases, forming sub-subclasses EC 3.1.11–16, that catalyses the hydrolysis of terminal diester linkages in polynucleotides to yield mononucleotides, the degradation of the chain occurring sequentially from one end. *Compare* **endonuclease**. *See also* **deoxyribonuclease**, **nuclease**, **ribonuclease**.

exopeptidase any enzyme of a group of peptide hydrolases within subclass EC 3.4 that catalyses the hydrolysis of peptide bonds adjacent to the terminal amino or carboxyl group of an oligo- or polypeptide. They include: EC 3.4.11, aminopeptidases; EC 3.4.13, dipeptidases; EC 3.4.14, di- and tripeptidyl peptidases; EC 3.4.15, peptidyldipeptidases; EC 3.4.16, serine-type carboxypeptidases; EC 3.4.17, metallocarboxypeptidases; EC 3.4.18, cysteine-type carboxypeptidases; and EC 3.4.19, omega peptidases.

exophthalmic goitre *or* **Graves' disease** a form of hyperthyroidism characterized by enlargement of the thyroid gland and protrusion of the eyeballs.

exopolysaccharide any of a range of extracellular homo- or heteropolysaccharides produced by microorganisms, either as insoluble capsules or as soluble slimes. They serve for protection and possibly also in recognition by host organisms.

exoribonuclease *see* **ribonuclease**.

exorphin any peptide with morphine-like activity (*see* **opioid peptide**) that originates from outside the body. Such substances occur, e.g., in proteolytic digests of certain dietary proteins. *Compare* **endorphin**.

exo-α-sialidase EC 3.2.1.18; *other names*: sialidase; neuraminidase; *N*-acylneuraminate glycohydrolase; α-neuraminidase; an enzyme that catalyses the hydrolysis of α-2,3-, α-2,6-, and α-2,8-glycosidic linkages joining terminal nonreducing *N*- or *O*-acylneuraminyl residues to galactose, oligosaccharides, glycoproteins or glycolipids. Examples: hemagglutinin–neuraminidase from measles virus (strain aik-c) (subacute sclerosing panencephalitis virus): database code HEMA_MEASA, 617 amino acids (69.24 kDa); sialidase (neuraminidase) from *Clostridium perfringens*: database code NANH_CLOPE, 382 amino acids (42.76 kDa).

exoskeleton any skeleton covering the outside of an organism or lying in the skin, such as the hard chitinous cuticle of an arthropod or the shell of a mollusc. *Compare* **endoskeleton**.

exosmosis the osmotic flow of water or of an aqueous solution from a cell, vessel, or organism into the surrounding aqueous medium. *Compare* **endosmosis**. —**exosmotic** *adj.*

exosome a fragment of exogenous DNA that, when taken up by a cell, is not readily integrated into the chromosome but can replicate, and be expressed.

exothermic describing a process or reaction that is accompanied by the evolution of heat; i.e. a process or reaction for which the change in enthalpy, ΔH, is negative at constant pressure and temperature. *Compare* **endothermic**.

exotic describing an introduced (i.e. foreign), nonendemic, nonacclimatized organism.

exotoxin any toxin formed by a microorganism and secreted into the surrounding medium. *Compare* **endotoxin**.

exp *(in mathematics) symbol for* exponential; *see* **exponential function**.

expansin any of a group of proteins, located within the cell walls of plants (both dicotyledons and grasses), that play an essential role in loosening cell walls during cell growth. They are hydrophobic, nonglycosylated proteins of $M_r \approx 30$ kDa.

experiment *abbr.*: expt.; **1** any procedure or series of procedures, carried out in defined conditions and designed to obtain new information about substances, materials, organisms, or natural phenomena, or to test or confirm a hypothesis. **2** *an alternative term for* **experimentation**. **3** to carry out an experiment or experiments. —**experimenter** *n.*

experimental *abbr.*: exptl.; **1** of, relating to, or based on the results of, an experiment or experimentation. **2** describing a disease produced deliberately in laboratory plants or animals for the purposes of study or as a model for the natural disease condition. **3** any particular object or system in an experiment that includes, or is subjected to, one of the variables. *Compare* **control** (def. 1). —**experimentally** *adv.*

experimentation the act, process, or practice of carrying out an experiment or experiments.

explant **1** to transfer a piece of living tissue from its normal situation to a culture medium. **2** any piece of tissue treated in this way. —**explanted** *adj.*

exponent *or* **index** *(in mathematics)* any number (or expression, or symbol for a number) indicating the power to which another number (or expression or symbol) is raised; e.g., in the expression a^n, n is the exponent, indicating that a is multiplied by itself n times.

exponential *(in mathematics)* **1** of, containing, or involving one or more exponents, e.g. an exponential equation. **2** de-

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scribing something approximately expressible by an exponential equation.

exponential function *(in mathematics)* any function of the type e^x or Ae^{ax}, where A and a are constants, e is an irrational number that is the base of natural logarithms, and x is a variable; e^x is sometimes written exp x.

exponential growth *an alternative term for* **logarithmic growth**.

exponential phase *an alternative term for* **logarithmic phase**.

export *informal term* describing a substance synthesized in, and then secreted from, a cell or type of cell in a multicellular organism; e.g. export protein.

exposure **1** *(in photography or radiography)* the act or process of exposing sensitized photographic material, e.g. a film or plate, to light or to ionizing radiation. **2** *(in photography)* **a** a measure of the amount of light admitted into a photographic device expressed in terms of the lens aperture (f number) and time. **b** *or* **light exposure** *symbol*: H; a physical quantity equal to the product of the illuminance and the time, Δt, for which the area is exposed. The SI unit is the lux second. **3** *(in radiation dosimetry)* a measure of the amount of X- or gamma radiation to which a subject or object is exposed, expressed in terms of the quantity of electric charge of the ions of one sign produced when all the electrons of both signs liberated in a volume of air of unit mass are completely stopped. The SI unit is C kg^{-1}, which has replaced the **röntgen**. *Compare* **absorbed dose**.

express **1** *(in genetics)* **a** to allow or cause the information in a gene to become manifest. **b** to activate the cellular functions involved in **gene expression**. **c** *(in cDNA technology)* to effect the synthesis of protein from the corresponding cloned gene using an **expression vector** in an **expression system**. **2** *(in mathematics)* to indicate by means of a symbol, formula, or equation. **3** to force or squeeze out a liquid from an object.

expressed sequence tag *abbr.*: EST; a partial sequence of a clone picked at random from a cDNA library and used in the identification of genes being expressed in a particular tissue. The technique exploits recent advances in automated DNA sequencing and sequence data handling, and a remarkably high number of ESTs turn out to represent previously unknown genes. These are identified by the predicted primary structure of the proteins that would be expressed and their relation to proteins of known structure. ESTs have proved extremely valuable in mapping the human genome, and there has been controversy surrounding attempts to patent them.

expression **1** the act or process of allowing information to become manifest. *See* **gene expression**, **expression vector**, **expression system**. **2** *(in mathematics)* a variable function or some combination of constants, variables, and/or functions. **3** the act or process of forcing or squeezing fluid from or out of something.

expression system a cell system into which an **expression vector** has been introduced and that contains all the enzyme systems needed for translation of messenger RNA. Ideally, it also contains the enzymes needed for post-translational modification of the synthesized protein. Expression in *Escherichia coli* or other bacterial cells may be inadequate for eukaryotic protein expression, but expression in mammalian cell lines may be inconvenient. Use of a baculovirus expression vector in insect cells is one technique that has been used successfully for eukaryotic protein expression.

expression tagged site *see* **ETS**.

expression vector *(in cDNA technology)* a **vector** that promotes transcription of a cloned gene, leading to synthesis of protein in a suitable **expression system**. An expression vector carries a **promoter**, e.g. *Eco*RI(UV5), which includes the regulatory region of the *lac* operon and the UV5 mutation, so that the system is insensitive to catabolite repression.

expressor a chemically undefined positive regulator of eukaryotic gene expression.

expt. *abbr. for* experiment (def. 1).

exptl. *abbr. for* experimental (def. 1, 2).

extein a peptide counterpart of an **exon**. *See* **intein**, **splicing**.

extended X-ray absorption fine structure (spectroscopy) *abbr.*: EXAFS (spectroscopy); a method for determining short-range order and local structure around specific atoms in noncrystalline materials. In this technique the X-ray absorption spectrum of the material is measured over an extended energy range near the absorption edge of one particular element in the material and structural details may be obtained from the observed modulation of the X-ray absorption on the high-energy side of the absorption edge. It is useful for elucidating the environment of metal ions in biological macromolecules.

extensin a glycoprotein found in plant cell walls in association with pectin. It resembles collagen of animal cells in being rich in *trans*-4-hydroxy-L-proline residues, and it contains L-arabinofuranose and D-galactopyranose residues attached in oligosaccharide units to the hydroxyl groups of the protein.

extension sequence a terminal sequence of amino-acid residues that is present in a nascent polypeptide as generated by translation of mRNA but is absent from any mature polypeptide or protein formed from it. An N-terminal extension sequence may be a signal sequence.

extensive property any of the properties of a substance or object that depend on the amount of the substance or the size of the object being considered, e.g. internal energy, mass, volume. *Compare* **intensive property**.

externalize *or* **externalise** to render external, especially to secrete a substance from a cell or organism. —**externalization** *or* **externalisation** *n.*

external standard any standard that is added to a sample at some point in an assay and serves as a reference by which the unknown being investigated can be quantified or identified.

external-standard method of quench correction *or* **external standardization** a method for correcting for quenching in **liquid scintillation counting** in which a source of gamma radiation external to the sample is brought into proximity with it after the sample has been counted and the sample is then counted again. The observed increase in count rate is correlated with that obtained using a set of differently quenched standards and the appropriate correction to the sample-count rate obtained. The method is simple and can be automated but on its own is less accurate than other methods. *Compare* **internal-standard method of quench correction**.

extinction *an older term (no longer recommended) for* **absorbance**.

extinction angle in **flow birefringence** between concentric cylinders, with polarizer and analyser at right angles, the angle between the **cross of isocline** and the cross formed by the polarizer and the analyser. It ranges from 45° (no orientation) to zero (complete orientation).

extinction coefficient *symbol* E; *an alternative term (no longer recommended) for* molar (decadic) absorption coefficient. *See* **absorption coefficient**.

extra- *prefix* signifying outside or beyond.

extra arm *or* **variable arm** the base-paired segment of variable length in the cloverleaf model of some tRNA molecules. *See* **transfer RNA**.

extracellular present outside a cell, expelled from a cell, or happening outside a cell. *Compare* **exocellular**, **intracellular**.

extracellular fluid *abbr.*: ECF; the portion of the total liquid content that occurs outside the cells, esp. as distinct from **intracellular fluid**. In higher animals it comprises the **interstitial fluid**, the **lymph**, and the **blood plasma**. In a 70 kg man the volume of ECF is approximately 15.5 L and it represents approximately 22% of body mass. *Compare* **intracellular fluid**.

extracellular matrix a layer consisting mainly of proteins (especially collagen) and glycosaminoglycans (mostly as proteoglycans) that forms a sheet underlying cells such as endothelial and epithelial cells. The constituent substances are secreted by cells in the vicinity, especially fibroblasts.

extracellular space that part of a multicellular organism outside the cells proper – usually taken to be outside the plasma membranes – and occupied by fluid.

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extrachromosomal describing structures, including DNA molecules, that are not part of a chromosome, or processes that proceed outside the chromosomes.

extrachromosomal inheritance inheritance controlled by extrachromosomal genes, such as those in mitochondrial or chloroplast DNA or in plasmids.

extract **1** to remove from or separate; to obtain a substance from a material, mixture, organism, or part of an organism by some chemical and/or physical process. **2** something extracted; a solution containing an active principle that has been extracted from plant or animal material.

extraction **1** the act or process of extracting. **2** something that has been extracted. *Compare* **extract** (def. 2).

extra piece *an alternative name for* **signal peptide**.

extrapolate *(in mathematics)* to estimate a value or the value of a function beyond the data values already obtained by either extending a graph or by calculation. *Compare* **interpolate**. —**extrapolation** *n.*

extremophile an organism that requires extreme physicochemical conditions for its optimum growth and proliferation. Such organisms include **thermophiles** or **psychrophiles**, **halophiles**, **alkalophiles** or **acidophiles**, **osmophiles**, and **barophiles**, based on their growth at extremes of temperature, salt concentration, pH, osmolarity, or pressure, respectively.

extrinsic originating or acting from the outside. —**extrinsically** *adv.*

extrinsic factor *a former name for* **vitamin B_{12}**.

extrinsic fluorescence fluorescence caused by a molecule of a fluor of small molar mass attached by either chemical coupling or simple binding to a (macro)molecule under study.

extrinsic pathway (of blood coagulation) *see* **blood coagulation**.

extrinsic protein *an alternative name for* **peripheral (cell membrane) protein**.

extrude to squeeze or force out; used especially of a solid or semisolid material. —**extrusion** *n.*

extrusome an organelle excreted as an anterior vacuole by a parasitic protist. It contains substances used for penetration of host cells.

ex vivo describing any biological process, reaction, or experiment in which the nature or magnitude of a change occurring in living tissues in intact organisms is subsequently measured ***in vitro*** following the excision of affected tissues. *Compare* ***in vivo*** [*Latin*, meaning from life.]

eye *(in molecular biology)* a region of DNA undergoing replication, in which the separated strands give the appearance of an eye.

***E/Z* convention** a convention of stereochemical descriptors for an unsaturated compound showing *cis–trans* isomerism that indicate unequivocally the steric relations around a (given) double bond. The **sequence rule** is applied in turn to the pair of atoms or groups attached to one of the doubly bonded atoms and to the pair attached to the other doubly bonded atom, and the order of preference in each case is established. If the two preferred atoms or groups are on opposite sides of the reference plane of the molecule the arrangement is called *E* [from German *entgegen*, opposite], and if they are on the same side of the plane it is called *Z* [from German *zusammen*, together]. For use as a prefix (in chemical nomenclature) the descriptor is placed in parentheses and connected with a hyphen, e.g. (*E*)-butenedioate and its stereoisomer (*Z*)-butenedioate (the respective systematic names for *trans*-1,2-ethylenedicarboxylate (= fumarate) and for *cis*-1,2-ethylenedicarboxylate (= maleate)). When a molecule of an unsaturated compound contains more than one double bond the prefix is composed of multiple symbols, each preceded if appropriate by the lower-numbered locant of the relevant double bond; e.g. (2*E*,4*Z*)-2,4-hexadienoate. The convention is now generally preferable to that using the structural prefixes *cis-* and *trans-*, especially for olefinic compounds having more than two substituents at a double bond (where it avoids possible ambiguity as to which pair of substituents is being designated). *See also* ***pro-E,pro-Z* convention**.

ezrin *or* **cytovillin** *or* **villin-2** *or* **P81** a protein involved in connections of major cytoskeletal structures to the plasma membrane, having domains in common with **talin**. It undergoes tyrosine phosphorylation after activation of specific growth factor receptors, and functions as a membrane-to-cytoskeleton linker that is involved in assembly of apical microvilli in parietal cells. It participates in the regulation of acid secretion. Example from human: database code EZRI_HUMAN, 585 amino acids (69.19 kDa).

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Ff

f *symbol for* femto+ (SI prefix denoting 10^{-15} times).

f *symbol for* **1** frequency (alternative to ν). **2** activity coefficient referenced to Raoult's law. **3** fugacity (alternative to $\tilde{p}$). **4** frictional coefficient. **5** furanose form (added after the symbol for a monosaccharide, e.g. Ara*f* for arabinofuranose). **6** *(in mathematics)* function.

F *symbol for* **1** a residue of the α-amino acid L-phenylalanine (alternative to Phe). **2** fluorine. **3** the fluoro group in an organic compound. **4** *(in genetics)* filial generation. **5** farad. **6** Fick unit. **7** *abbr. for* fertility; *see* **F plasmid**. **8** *abbr. sometimes used* (not recommended) to designate **folate** or folic acid or their reduced derivatives.

F1, F2a1, F2a2, F2b, F2c, F3 *older nomenclature for* **histones**. F signifies fraction; in early work, the histones were extracted from the nuclei with sulfuric acid solutions, and separated according to their solubility.

F_{420} *see* **coenzyme F_{420}**.

F_{430} *see* **coenzyme F_{430}**.

°F *symbol for* degree Fahrenheit. *See* **Fahrenheit temperature scale**.

F^+ *symbol for* a donor bacterial cell containing an **F plasmid**; F^- denotes a recipient bacterial cell lacking an F plasmid.

F *symbol for* **1** Faraday constant. **2** force (bold italic in vector equations). **3** fluence (alternative to *H*).

FA *abbr. for* **1** fatty acid. **2** folic acid or folate (not recommended). **3** filtrable agent.

Fab fragment a ≈45 kDa protein fragment obtained (together with **Fc fragment** and **Fc′ fragment**) by papain hydrolysis of an **immunoglobulin** molecule. It consists of one intact light chain linked by a disulfide bond to the N-terminal part of the contiguous heavy chain (the **Fd fragment**). Two Fab fragments are obtained from each IgG antibody molecule; each fragment contains one antigen-binding site. The term Fab is derived from ['fragment antigen-binding']. *Compare* **$F(ab)_2$ fragment**. *See also* **Fv fragment**.

$F(ab')_2$ fragment a ≈90 kDa protein fragment obtained (together with **pFc′ fragment**) by pepsin hydrolysis of an **immunoglobulin** molecule. It consists of that part of the immunoglobulin molecule N-terminal to the site of pepsin attack and contains both **Fab fragments** held together by disulfide bonds in a short section of the **Fc fragment** (the hinge region). One $F(ab')_2$ fragment is obtained from each IgG antibody molecule; it contains two antigen-binding sites but not the site for complement fixation. *Compare* **Fab fragment**.

FABP *abbr. for* fatty acid binding protein (e.g. **albumin**, etc.); four motifs are characteristic of this function.

Fabry's disease an X-linked inborn error of human metabolism due to defective lysosomal α-D-galactosidase A activity. It is a **sphingolipidosis** or sphingolipid lysosomal storage disease. The enzyme defect leads to the progressive deposition in most visceral tissues of neutral glycosphingolipids with terminal α-D-galactosyl residues, principally globotriaosylceramide, Gal(α1-4)Gal(β1-4)Glc(β1-1)Cer. [After Johannes Fabry (1860–1930), German physician.]

facilitated diffusion diffusion (def. 2) across a biological membrane through the participation of specific transporting agents (transporters) or carriers. The equilibrium distribution reached is the same as that achieved by **simple diffusion** but at any one site facilitated diffusion is mediated by a transport protein that exhibits specificity for the transported species. The existence of the transporter mediates passage across the membrane of molecules to which it would otherwise be impermeable. *Sometimes termed* **mediated transport** to distinguish it from **active transport**.

FACIT *abbr. for* fibril-associated collagens with interrupted triplex helices; a group of collagens (types IX, XII, and XIV) composed of triple-helical regions interrupted by non-triple-helical regions of 8–42 amino acids.

FACS *abbr. for* fluorescence-activated cell sorter.

F-actin the form of **actin** found in filaments.

factor **1** any component or cause that contributes to an effect or result; a term often used to denote an uncharacterized (or incompletely characterized) component of a biological system. **2** *(in mathematics)* any integer or polynomial that can be divided exactly into another integer or polynomial.

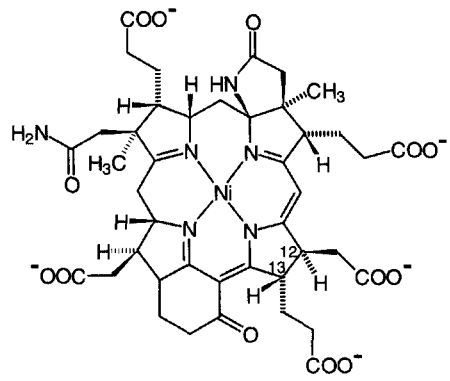
factor I to factor XIII, factor Va, etc. names of the **blood coagulation** factors.

factor B a component of **complement**.

factor D a component of **complement**.

factor F *an alternative name for* **initiation factor**.

factor F_{430} a nickel-containing tetrapyrrole compound involved in the terminal reductive step of methanogenesis in **methanogenic** bacteria, in which methane is formed from methyl-coenzyme M (*see* **coenzyme M**). It exists both as the protein-bound and free forms. The free form has an absorption maximum at 430 nm, which shifts to 421 nm in the bound form.



factor G *an alternative name for* **EF-G**; *see also* **elongation factor**.

factor H a component of **complement**.

factor I a component of **complement**.

factorial *symbol*: !; the product of all positive integers from 1 up to and including the integer in question, *n*; hence

$$n! = n(n-1)(n-2)(n-3)\ldots 3 \times 2 \times 1.$$

factor IF *an alternative name for* **initiation factor**.

factor R *an alternative name for* **release factor**.

factor S a tetrapeptide, of unknown structure, isolated from cerebrospinal fluid of goats, that slowly induces delta (slow wave) sleep in rats on infusion into the cerebral ventricles.

factor T *an alternative name for* **EF-T**; *see also* **elongation factor**.

facultative able to live under more than one set of environmental conditions.

facultative aerobe *see* **aerobe**.

facultative anaerobe *see* **anaerobe**.

FAD *abbr. for* flavin-adenine dinucleotide.

fade the waning of a response in the continued presence of an agonist. *Compare* **desensitization**.

$FADH_2$ *abbr. for* flavin-adenine dinucleotide (reduced).

F agent *see* **sex factor**.

Fahrenheit temperature scale a temperature scale in which 32 °F is set equal to 273.15 K and 212 °F is set equal to 373.15 K. Thus 1 Fahrenheit degree = 5/9 × K, and Fahrenheit tem-

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perature (°F) = 9/5 × (Celsius temperature) + 32. [After G. D. Fahrenheit (1686–1736), German scientist.]

fall curve the curve describing the decrease in the colour intensity of a sample with time, obtained in a colorimetric analysis using an autoanalyser.

falling-drop method a method for the accurate determination of relative densities of liquids in which a drop of the liquid is allowed to fall to its equilibrium position in a column containing a defined density gradient of an immiscible liquid. It was formerly used for determination of the deuterium oxide content of samples of water.

falling-mercury electrode *an alternative term for* **dropping-mercury electrode**.

falling-sphere viscometer an instrument for measuring the viscosity of a liquid from the time taken for a solid sphere to fall through a given distance in a column of the liquid compared with the time taken for it to fall through the same distance in a liquid of known viscosity.

Fallopian tube an **oviduct** of a mammal.

familial **1** of or pertaining to a given family. **2** describing something transmitted between members of a family, especially a familial character, condition, or disease.

family **1** *(in taxonomy)* a taxonomic category of related organisms ranking below the **order** and above the **genus**. **2** *(in chemistry and biochemistry) an imprecise term for* a group of substances closely related structurally. *See also* **superfamily**. **3** *(in molecular biology) see* **Appendix E**.

Fanconi syndrome an inherited human disorder characterized by glycosuria, amino aciduria, phosphaturia, and acidosis. It is due either to functional deficiency of the proximal renal tubules or to abnormalities in amino-acid metabolism. *See also* **renal rickets**. [After Guido Fanconi (1892–1979), Swiss pediatrician.]

farad *symbol*: F; the SI derived unit of electric capacitance. A capacitor has a capacitance of one farad when a charge of one coulomb raises the potential between its plates to one volt: i.e. 1 F = 1 C V^{-1}. [After Michael Faraday (1791–1867), British physicist.]

faradaic current an electric current flowing through an electrode that corresponds to the electrolytic oxidation or reduction of one or more chemical species.

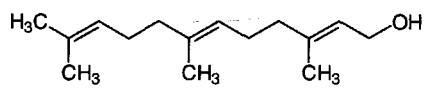
Faraday constant *symbol*: *F*; a fundamental constant, defined as the quantity of electricity required to deposit one mole of a univalent ion from a solution of an electrolyte. It is the arithmetic product of the Avogadro constant, *L* (or N_A), and the elementary charge, *e*; hence

$$F = Le \text{ (or } F = N_A e) = 9.648\ 530\ 9(29) \times 10^4 \text{ C mol}^{-1}.$$

Faraday effect the rotation of the plane of vibration of polarized light, or of other polarized electromagnetic radiation, when passing through an isotropic, transparent medium in a magnetic field that has a component in the direction of the radiation.

Farber's disease *or* **Farber's lipogranulomatosis** *an alternative name for* **ceramidase** deficiency.

farnesol *the trivial name for* any of four possible stereoisomers of 3,7,11-trimethyl-2,6,10-dodecatrien-1-ol; a sesquiterpene alcohol. The 2*E*,6*E*-isomer is found in many essential oils. The 2*Z*,6*E*-isomer is a minor constituent of some essential oils.



2*E*,6*E*-isomer

farnesyl the (2*E*,6*E*)-3,7,11-trimethyl-2,6,10-dodecatrien-1-yl group; the alkenyl group derived from the sesquiterpene alcohol **farnesol**. 2*E*,6*E*-Farnesyl diphosphate (= *trans,trans*-farnesyl diphosphate) is an intermediate in carotenoid, sesquiterpene, squalene, and sterol biosynthesis and is also a substrate in the addition of the farnesyl group to proteins (*see* **prenylation**).

farnesyltransferase EC 2.5.1.21; *recommended name*: farnesyl-diphosphate farnesyltransferase; *systematic name*: farnesyl-diphosphate:farnesyl-diphosphate farnesyltransferase; *other name*: presqualene-diphosphate synthase. An enzyme that catalyses the formation of presqualene diphosphate from two molecules of farnesyl diphosphate with release of pyrophosphate. It occurs in the pathway for the synthesis of **squalene** and derivatives (cholesterol, sesquiterpenes). In eukaryotes it is a monomeric microsomal enzyme. Example from yeast: database code ERG9_YEAST, 444 amino acids (51.61 kDa).

farnesyl*trans*transferase EC 2.5.1.29; *systematic name*: *trans,trans*-farnesyl-diphosphate:isopentenyl-diphosphate farnesyl*trans*transferase; *other name*: geranylgeranyl-diphosphate synthase. An enzyme that catalyses the formation of geranylgeranyl diphosphate from *trans,trans*-farnesyl diphosphate and isopentenyl diphosphate with the release of pyrophosphate. It occurs in the pathway for sesquiterpene and cholesterol synthesis and forms the **prenyl** derivative geranylgeranyl diphosphate. In some fungi and plants this activity is part of a multifunctional protein that also has the activities of geranylgeranyl-diphosphate synthase (*see* **dimethylallyl*trans*transferase**) and **geranyl*trans*transferase**. Example from *Neurospora crassa*: database code GGPP_NEUCR, 428 amino acids (47.83 kDa).

farnoquinone *an alternative name for* menaquinone-6; *see* **menaquinone**.

Farr test a **radioimmunoassay** technique for measuring the absolute antigen-binding capacity of an antiserum. The antibody is allowed to react with radiolabelled antigen and the antigen–antibody complex is then precipitated by addition of saturated ammonium sulfate solution to a final concentration of 40% w/v. The antigen that has reacted can be determined in the precipitate.

far ultraviolet *see* **ultraviolet**.

fascicle *or* **fibre tract** a tight parallel bundle of nerve fibres that are either axons or dendrites. It is formed during the growth of nerves, and is mediated in part by cell **adhesion molecules**.

fasciclin any of the proteins of a related group that are involved in nerve **fascicles** (bundles). They include fasciclin I, a neuronal cell **adhesion molecule**; example (precursor) from *Drosophila melanogaster*: database code FAS1_DROME, 652 amino acids (72.52 kDa); and fasciclin II, which is a neuronal recognition molecule related to NCAM (*see* **adhesion molecules**): database code FS21_DROME, 873 amino acids (96.82 kDa).

fascin a protein involved in the formation of actin bundles and actin polymerization. Example from *Strongylocentrotus purpuratus*: database code SUSFASCIN, 496 amino acids (54.88 kDa).

fast **1** (*of a component of a mixture or specified substance*) one that migrates further or furthest from the origin in chromatography or electrophoresis. **2** uninfluenced by a specified agent, e.g. by light, acid, etc. *See also* **acid-fast bacilli**. **3** to abstain from, or to be prevented from, taking nourishment for at least 24 hours (in the case of laboratory animals). In clinical chemistry, the requirement is often for an overnight fast, normally at least 10 hours. —**fasted** *adj.*; —**fasting** *n.*

FASTA *or* **FASIN** a computer program used for searching and analysing protein and nucleic acid sequences.

fast component an unusual component of a mixture, e.g. a hemoglobin variant, that moves in a specified buffer system more rapidly in chromatography or electrophoresis than does the normal component.

fast reaction any reaction, or step in a reaction sequence, that has a large rate constant and proceeds rapidly. In a reaction sequence, a fast reaction is not the rate-limiting step.

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fat **1** any triacylglycerol or mixture of triacylglycerols that is solid below 20 °C; those that are liquid at such temperatures are usually referred to as oils. **2** *an alternative name for* **lipid**. **3** *an alternative name for* adipose tissue; *see* **brown adipose tissue**, **white adipose tissue**.

fatal familial insomnia a rare inherited neurological disease, first described in 1986 among inhabitants of mountainous regions of Italy. It is characterized by intractable insomnia and other neurological abnormalities. It is one of three familial forms of human **prion** disease. Neuropathologically, there is neuronal loss with associated gliosis. It is associated with a pathogenic mutation of the prion gene at codon Asn^{178} (shared with Creutzfeldt–Jakob disease, but for unknown reasons of different phenotype) linked to codon Met^{129}, a site that exhibits Met/Val polylmorphism.

fat body any of the fat-containing cellular structures that serve as energy reserves in amphibians, insects, and reptiles.

fat cell *or* **fat-cell** *or* **lipocyte** *or* (*in animals*) **adipocyte** any living cell containing noticeable amounts of lipid, primarily as fat or oil.

fat index the mass of diethylether-extractable fat per unit mass of nonfat material (on a dry-weight basis) in, e.g., a foodstuff or tissue.

F_1-ATPase *see* **H^+-transporting ATP synthase**.

fat-soluble vitamin any of a diverse group of **vitamins** that are soluble in organic solvents and relatively insoluble in water. The group includes vitamins A, D, E, and K.

fat solvent any **lipid solvent** e.g. chloroform or diethylether, that will extract triacylglycerols from biological or other materials.

fatty derived from or containing fat.

fatty acid any of the aliphatic monocarboxylic acids that can be liberated by hydrolysis from naturally occurring fats and oils. Fatty acids are predominantly straight-chain acids of 4 to 24 carbon atoms, which may be saturated or unsaturated; branched fatty acids and hydroxy fatty acids also occur, and very long chain acids of over 30 carbons are found in waxes. *See also* **fatty-acid nomenclature**, **polyunsaturated fatty acid**.

fatty-acid activation the conversion of a fatty acid molecule to its fatty acyl-coenzyme A thioester, the first step in the reactions of **beta oxidation**. Fatty acyl-coenzyme A can be formed in a reaction catalysed by the acid-thiol ligases EC 6.2.1.1, 6.2.1.2, and 6.2.1.3, or by a CoA-transferase of sub-subclass EC 2.8.3.

fatty-acid nomenclature a system of symbols for describing fatty acids. The basic symbolism comprises the number of carbon atoms in the molecule, followed by the number of double bonds; the two numbers are separated by a colon. Thus, 16:0 represents palmitic acid, 16:1 palmitoleic acid, etc. To avoid ambiguity, double bond positions in unsaturated fatty acids should be indicated; 18:3 (9,12,15) represents α-linolenic acid, 18:3 (9,11,13) represents eleostearic acid. These symbols may also include the *E*/*Z* configurational descriptors (see ***E*/*Z* convention**). Although not now recommended, a still used system numbers the first double bond from the carboxyl group using the Greek letter Δ. Thus, oleic acid is 18:1 $\Delta 9$ or 18:1 Δ^9. This system persists in some enzyme names; e.g., the systematic name for linoleate isomerase (EC 5.2.1.5) is linoleate Δ^{12}-*cis*-Δ^{11}-*trans*-isomerase. *See also* **fatty acid oxidation complex**. Double bonds may also be designated from the end of the chain remote from the carboxyl group. If *n* is the total number of carbons, *n*-3 represents CH_3–CH_2–CH=CH–, etc. Since in many unsaturated fatty acids the double bonds are successively separated by methylene groups, only the position of the first double bond may be given. Thus linoleic acid [18:2 (9,12)] is also represented as 18:2 *n*-6. The Greek letter ω has also been used in the same way; e.g. for linoleic acid, 18:2 ω-6. However, it is not recommended that a double bond position, e.g. that of oleic acid, should be designated as ω9. *See also* **fish oil**, **linoleic family**, **linolenic family**, **oleic family**, **palmitoleic family**.

fatty-acid oxidation complex a bacterial multifunction protein complex that catalyses the **beta oxidation** of fatty acids. The example from *Escherichia coli* comprises α and β subunits. The α subunit contains **decenoyl-CoA Δ-isomerase**, **enoyl-CoA hydratase**, **3-hydroxyacyl-CoA dehydrogenase**, and 3-hydroxybutyryl-CoA epimerase; database code FADB_ECOLI, 729 amino acids (79.50 kDa). The β subunit contains 3-ketoacyl-CoA thiolase; database code THIK_ECOLI, 387 amino acids (40.84 kDa). For a mammalian system *see* **beta-oxidation system**.

fatty acid synthase complex a large, well-defined multienzyme complex found in eukaryotes. These enzyme complexes, which are cytoplasmic, catalyse a cyclic set of reactions whereby fatty acids are synthesized from one molecule of acetyl coenzyme A and successive molecules of malonyl coenzyme A. In *Escherichia coli* and most bacteria the activities are in separate proteins. In animals, the enzyme complex (EC 2.3.1.85) produces a long-chain fatty acid (typically palmitate), whereas in yeast the product is a long-chain-fatty-acyl-CoA. The synthase complex of yeast has a mass of 2300 kDa and appears in the electron microscope as an ellipsoid, 25 μm long and 21 μm in cross section. The yeast enzyme comprises α and β subunits. It is termed fatty-acyl-CoA synthase (EC 2.3.1.86), and catalyses the overall reaction:

acetyl-CoA + *n* malonyl-CoA + 2*n* NADH + 2*n* NADPH = a long-chain-acyl-CoA + *n* CoA + *n* CO_2 + 2*n* NAD^+ + 2*n* $NADP^+$;

To synthesize palmitoyl-S-[acyl-carrier protein] requires seven repetitions of the following set of reactions, where X = -S-[acyl carrier protein]:

(1) $R–CH_2–CO–X + {}^-OOC–CH_2–CO–X \rightarrow R–CH_2–CO–CH_2–CO–X + CO_2 + H–X$

(2) $R–CH_2–CO–CH_2–CO–X + NADPH \rightarrow R–CH_2–CH(OH)–CH_2–CO–X + NADP^+$

(3) $R–CH_2–CH(OH)–CH_2–CO–X \rightarrow R–CH_2–CH=CH–CO–X + H_2O$

(4) $R–CH_2–CH=CH–CO–X + NADH \rightarrow R–CH_2–CH_2–CH_2–CO–X + NAD^+$

The hydroxacyl product of reaction (2) has the 3*R* configuration and the enoylacyl product of reaction (3) has *E* configuration. Before the assembly begins, acetyl and malonyl units are transferred from their CoA derivatives to acylcarrier protein (ACP) by the activities of two transferases, EC 2.3.1.8 and EC 2.3.1.9. Representative enzyme activities for the four reactions are named as follows: reaction (1), EC 2.3.1.41, 3-oxoacyl-[ACP] synthase; reaction (2), EC 1.1.1.100, 3-oxoacyl-[ACP] reductase; reaction (3), EC 4.2.1.61, 3-hydroxypalmitoyl-[ACP] dehydratase; reaction (4), EC 1.3.1.9, enoyl-[ACP] reductase (NADH).

Similar enzymes with different chain length specificities may also be involved. For the first round, R = H, the two synthase substrates thus being acetyl-[ACP] and malonyl-[ACP]; the product is 3-oxobutanoyl-[ACP]. After seven repetitions of the four reactions, R = $C_{12}H_{25}$, and the product is palmitoyl-[ACP]. The yeast α subunit catalyses reactions (1) and (2); database code FAS2_YEAST, 1894 amino acids (207.86 kDa). The yeast β subunit catalyses the two acyl transfer reactions and reactions (3) and (4); database code FAS1_YEAST, 2051 amino acids (228.43 kDa).

The mammalian complex is a dimer of identical subunits (260 kDa). Since the product is palmitic acid itself a further enzyme is present: EC 3.1.2.14 (oleoyl-[ACP] hydrolase). Each polypeptide chain is folded into three domains: domain 1 contains the acyltransferase activities and catalyses reaction (1); domain 2 catalyses reactions (2), (3), and (4); domain 3 catalyses the hydrolysis of palmitoyl-[ACP] to palmitate. In liver, reaction (4) is catalysed by EC 1.3.1.39, **enoyl-[acyl-carrier-protein] reductase (NADPH, A-specific)**.

fatty-acid thiokinase *an alternative name for* **1** butyryl–CoA

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ligase (EC 6.2.1.2). **2** long-chain-fatty-acid–CoA ligase; *see* **fatty-acyl–CoA ligase**.

fatty-acyl-CoA dehydrogenase any of the acyl-CoA dehydrogenase components of the **beta-oxidation system**.

fatty-acyl-CoA desaturase *see* **stearoyl-CoA desaturase**.

fatty-acyl–CoA ligase either of two enzymes involved in fatty-acid activation.

(1) Long-chain-fatty-acid–CoA ligase (EC 6.2.1.3); *other names*: acyl-activating enzyme; acyl-CoA synthetase; fatty acid thiokinase (long-chain); lignoceroyl-CoA synthase. It catalyses a reaction between ATP, a long-chain carboxylic acid, and CoA to form an acyl-CoA and pyrophosphate. In mammals there are tissue isoforms. Example from rat liver: database code LCFA_RAT, 699 amino acids (78.09 kDa).

(2) Medium-chain-fatty-acid–CoA ligase (EC 6.2.1.–); *other name*: medium-chain-fatty-acid–CoA synthase. It catalyses the same reaction as above but with medium-chain fatty acids. Example from *Pseudomonas oleovorans*: database code ALKK_PSEOL, 546 amino acids (59.19 kDa).

fatty-acyl-CoA synthase **1** the multifunctional protein responsible for the synthesis of long-chain fatty acyl moieties in some eukaryotes, e.g. yeast. *See* **fatty acid synthase complex**. **2** an enzyme of the endoplasmic reticulum, EC 6.2.1.3, long-chain-fatty-acid–CoA ligase, that carries out a reaction between ATP, CoA, and a long-chain fatty acid to form the corresponding fatty-acyl CoA, AMP, and pyrophosphate.

fatty-acyl group any acyl group derived from a fatty acid.

fatty alcohol *an alternative term for* **long-chain alcohol**.

fatty degeneration *or* **fatty infiltration** the deterioration of a tissue due to the deposition of abnormally large amounts of fat, usually as globules, in its cells.

fatty liver a pathological condition of liver tissue that has undergone **fatty degeneration**. It results from administration of various poisons, especially chlorinated hydrocarbons, or as a result of a dietary deficiency of choline or threonine.

favism a disease of humans in which hemolysis is caused by eating fava beans (*Vicia faba*) or by certain drugs, e.g. sulfonamides, primaquine, and nitrofuran antibiotics. The basic defect is an inherited deficiency of glucose-6-phosphate dehydrogenase in the red blood cells; about 70 variants are known. *See also* **glucose-6-phosphate dehydrogenase deficiency**.

FBP *abbr. for* fructose 1,6-bisphosphate.

FCCP *abbr. for* carbonylcyanide *p*-trifluoromethoxyphenylhydrazone; an uncoupling agent.

F cell *a former name for* **PP cell**.

F_1-CF_0 the ε subunit of the **H^+-transporting ATP synthase** complex in the chloroplasts of *Chlamydomonas reinhardtii*, in which the subunit arrangement is different from that in higher plants.

Fc fragment a crystallizable protein fragment obtained (together with **Fab fragment**) by papain hydrolysis of an **immunoglobulin** molecule. That obtained from human IgG is a 50 kDa protein consisting of the C-terminal halves of two heavy chains linked by two disulfide bonds. The Fc fragment has no antigen-binding activity but carries sites for complement fixation. [Fc is from 'fragment-crystallizable'.] *Compare* **Fc′ fragment**, **Fd fragment**.

Fc′ fragment a protein fragment obtained in small amounts by papain hydrolysis of an **immunoglobulin** molecule, in addition to **Fab fragments** and **Fc fragment**. That obtained from human IgG is a 24 kDa protein; it forms noncovalently bonded dimers consisting of the C-terminal moieties of two Fc fragments minus their C-terminal tridecapeptide segments. It normally occurs in small quantities in human urine. *See also* **pFc′ fragment**.

Fc receptor any of a number of proteins that bind the Fc region of immunoglobulins A, E or G, and facilitate their recognition and uptake, especially by phagocytic cells (*see* **phagocyte**). Several types have been described; all of the proteins involved have a single transmembrane helical region. FcγR receptor I (*abbr.*: FcγRI) *or* CD64, is a high affinity receptor for IgG, capable of binding monomeric antibody. It is a characteristic marker of mononuclear phagocytes, but may also be expressed on activated neutrophils; example: database code FCGO_HUMAN, 347 amino acids (42.6 kDa). FcγRII *or* CD32 is a low affinity receptor for IgG present on monocytes, neutrophils, eosinophils, B cells and platelets. Crosslinking of the surface antibody and the receptor leads to downregulation of the B cell. Binding of immune complexes to this receptor leads to degranulation of platelets and release of inflammatory mediators; example: database code FCGA_HUMAN, 317 amino acids (34.99 kDa). Another low affinity IgG receptor, FcγRIII *or* CD16 is found on macrophages, polymorphs, eosinophils and NK cells. On large granular lymphocytes it is a transmembrane glycoprotein that can link the cells to antibody-sensitized target cells, while on macrophages and neutrophils it has a **GPI anchor**. Two types of IgE receptor are known: (1) a high affinity receptor, FcεRI, found on basophils and mast cells, which on activation leads to the release of histamine and the manifestation of allergy. It is a tetramer of one α chain, one β chain and two disulfide-linked γ chains, examples: α chain, database code FCEA_HUMAN, 257 amino acids (29.6 kDa); β chain, database code FCEB_HUMAN, 244 amino acids (26.53 kDa); γ chain, database code FCEG_HUMAN, 86 amino acids (9.67 kDa). (2) a low affinity receptor, FcεRII, found on lymphocytes and monocytes and involved in IgE production and differentiation of B cells. An IgA receptor is found on myeloid cells; example: database code FCAR_HUMAN, 287 amino acids (32.26 kDa).

FCS *abbr. for* fetal calf serum.

Fd *symbol for* ferredoxin.

Fd_{540} *symbol for* a membrane-bound **ferredoxin** with a redox potential of –0.54 V.

Fd_{590} *symbol for* a membrane-bound **ferredoxin** with a redox potential of –0.59 V.

FDA *abbr. for* Food and Drug Administration (of the USA).

Fd fragment a protein fragment obtained by papain hydrolysis of an **immunoglobulin** molecule followed by reduction of the disulfide bonds. It consists of the part of the **heavy chain** N-terminal to the papain hydrolysis site. The N-terminal moiety is variable and forms part of the original antigen-combining site; the C-terminal moiety is constant. *Compare* **Fc fragment**.

FDNB *abbr. for* fluorodinitrobenzene; **Sanger's reagent**.

FDP *abbr. for* fructose 1,6-diphosphate (now named **fructose 1,6-bisphosphate**).

FdU *abbr. for* fluorodeoxyuridine (the symbol FdUrd is recommended).

FdUrd *symbol for* (a residue of) the deoxyribonucleotide fluorodeoxyuridine (*see* **flurouracil**).

Fe *symbol for* iron.

Fe(II) *symbol for* ferrous (divalent) iron.

Fe(III) *symbol for* ferric (trivalent) iron.

FEBS *abbr. for* Federation of European Biochemical Societies.

fecal fat fat in the feces; the output of fecal fat is normally below about 18 mmol 24 h^{-1} in the adult human. Tests that measure the fat content of feces may assist in diagnosis of generalized malabsorption syndrome; an alternative method is the [^{14}C]**triolein breath-test**.

fed batch process a process during which one or more nutrients are supplied to a bioreactor, usually without removing biomass and products. *See* **batch process**.

Federation of European Biochemical Societies *abbr*: FEBS; an international scientific organization founded in 1964 and now representing some 32 countries, including all those of mainland Europe plus Israel. FEBS is governed by a Council composed of one delegate from each of the adhering national biochemical societies plus the members of the Executive Committee. FEBS organizes an annual meeting, advanced courses, and supports fellowships and three annual prizes. It publishes two journals, *FEBS Letters* and *European Journal of Biochemistry*.

feedback **1** any feature of a system, e.g. of a metabolic pathway or of an electronic circuit, whereby information about the

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output of the system is used to influence the input to that system. Such feedback may increase the input to the system – **positive feedback** – or reduce the input to the system – **negative feedback**. A cyclic system of components participating in feedback forms a **feedback loop**, and the system is known as a **closed-loop system**. *Compare* **open-loop system**. **2** that part of the output of an electronic, mechanical, or other system that is returned to the input, so modifying its characteristics. *Compare* **feedforward**. —**feed back** *vb.*

feedback control control of the activity of any system by a mechanism involving **feedback**.

feedback inhibition *or* **retroinhibition** inhibition of the activity of an enzyme by the accumulation of a substance produced further along a metabolic pathway of which the enzyme is a constituent. *Compare* **enzyme repression**, **feedback repression**.

feedback repression an inhibitory feedback system in which the accumulation of a substance produced in a metabolic pathway represses the synthesis of an enzyme that is required at an earlier stage of the pathway. *Compare* **enzyme repression**, **feedback inhibition**.

feeder cell an irradiated cell that is capable of metabolizing but not of dividing. Such cells are sometimes added to cultures of unirradiated cells to help in the provision of nutrients.

feeder layer a layer of **feeder cells** in a cell culture.

feeder pathway any (minor) metabolic pathway that supplies metabolites to another (major) metabolic pathway.

feedforward **1** any feature of a system, e.g. a metabolic pathway, whereby information about the input to the system is used to influence the output of the system. *Compare* **feedback** (def. 1). **2** that part of the input of a system that influences the output of the system.

Fehling's solution a test reagent for glucose and other reducing substances. It is prepared as two solutions: **Fehling's solution A** containing 0.278 M copper (II) sulfate, and **Fehling's solution B** containing approximately 1.65 M potassium sodium tartrate and 4.3 M potassium hydroxide; equal volumes of each solution are mixed before a test. When boiled with a reducing substance a yellow or red precipitate of copper (I) oxide is formed. *Compare* **Benedict's solution**. [After Hermann Christian von Fehling (1812–85), German organic chemist.]

feline of, pertaining to, or resembling cats.

felix a protein designed for theoretical modelling studies and expressed from a synthetic gene in *Escherichia coli*. Database code NRL_1FLX, 79 amino acids (8.77 kDa), which also gives the predicted 3-D structure. [From four-helix bundle.]

female *symbol*: ♀; **1** of, pertaining to, or designating the sex that only produces gametes that can be fertilized by male gametes. **2** describing a flower that lacks stamens or has nonfunctional stamens.

female sex hormones any of the **estrogens** (estradiol-17β, estrone, and estriol) that are concerned with the normal growth and development of the mammalian female reproductive tract and, together with **progesterone**, control the estrous and reproductive cycles.

FeMo-co *abbr. for* iron–molybdenum cofactor (of component I of **nitrogenase**).

FeMo protein any iron–molybdenum-containing protein.

FEMS *abbr. for* Federation of European Microbiological Societies.

femto+ *symbol*: f; SI prefix denoting 10^{-15} times.

femtomolar *(informal)* describing a solution containing 10^{-15} mol dm^{-3} (of a specified solute).

femtomole *symbol*: fmol; one 10^{-15}th part of a mole (of a specified substance).

F episome *an alternative name for* **F plasmid**.

Fe protein any iron-containing protein.

feral wild; having escaped from cultivation or domestication and reverted to the wild state.

ferment **1** any agent or substance that causes fermentation. **2** *a former name for* **enzyme**. **3** *an alternative name for* **fermentation**. **4** to undergo or to effect **fermentation**. —**fermentable** *adj.*; **fermentability** *n.*

fermentation **1** (or ferment) the decomposition of chemical substances, brought about by **ferments** (def. 1), resulting in the production of simpler substances and, often, of energy; an instance of this, especially the anaerobic breakdown of glucose to lactate or ethanol. **2** *(in biotechnology)* the use of microorganisms or cultured cells to produce useful materials, such as antibiotics, beverages, enzymes, and some commodity chemicals.

fermenter **1** *or* **fermentor** *or* **biofermenter** an apparatus or a vessel in which to conduct **fermentation** under more or less controlled conditions. **2** a person or other agent that causes or is able to cause fermentation. **3** a genus, species, or strain of microorganism that ferments (or does not ferment) glucose or a specified sugar; e.g. **lactose fermenter**, **non-lactose fermenter**.

fermentor *a variant spelling of* **fermenter** (def. 1).

Fernández-Morán particle another name for **elementary particle** (def. 2), attached to the cristae of the mitochondrion.

ferralterin a soluble nonheme, iron–sulfur-containing chloroplast protein, mediating the light activation of chloroplast fructose 1,6-bisphosphatase.

ferredoxin *symbol*: Fd; any simple, nonenzymic **iron–sulfur protein** that is characterized by having equal numbers of atoms of iron and labile sulfur (releasable as hydrogen sulfide by acidification). The iron and sulfur atoms are present in one or two clusters of two or four atoms of each. Ferredoxins are of M_r 6000–24 000; many have a particularly low redox potential ($E_o' = -0.2$ V to -0.6 V). They act as electron carriers in a variety of oxidation–reduction systems and have been found in a wide range of microorganisms, in chloroplasts, and in mitochondria from adrenal cortex (*see* **adrenodoxin**) and heart muscle. Example: 2Fe-2S type from *Spirulina platensis*: database code NRL_3FXC, 98 amino acids (10.49 kDa); three conserved motifs; 3-D structure known. *Compare* **rubredoxin**. *See also* **high-potential iron–sulfur protein**, **nitrogenase**.

ferredoxin-NADP$^+$ reductase *another name for* **NADPH:adrenodoxin oxidoreductase**.

ferredoxin–nitrite reductase *see* **nitrite reductase**.

ferri+ *comb. form* denoting containing ferric iron.

ferric of or containing trivalent iron, Fe^{3+} or Fe(III).

ferrichrome any of a group of growth-promoting Fe(III) chelates formed by various genera of microfungi, e.g. species of *Aspergillus*, *Neurospora*, and *Ustilago*. They are homodetic cyclic hexapeptides made up of a tripeptide of glycine (or other small neutral amino acids) and a tripeptide of an N^4-acyl-N^4-hydroxy-L-ornithine (e.g. the N^4-acetyl compound). They are thus **siderochromes** of the hydroxamic-acid-derivative category.

ferricytochrome any **cytochrome** in which the iron atom is in the ferric form.

ferriheme *or (esp. UK)* **ferrihaem** any Fe(III)–porphyrin coordination complex.

ferriheme chloride *another name for* **hemin**.

ferriheme hydroxide *another name for* **hematin**.

ferrihemochrome any **hemochrome** containing Fe(III).

ferrihemoglobin *or* **methemoglobin** (*abbr.*: MetHb) an oxidation product of hemoglobin in which all its four iron atoms are in the ferric, Fe(III), state, the sixth coordination valencies of which are occupied, in the acid form, by water molecules, or, in the alkaline form, by hydroxide ions; these two forms have characteristic absorption spectra. Unlike hemoglobin, it cannot bind and transport dioxygen. The 3-D structure is known (Brookhaven file 1HGB.PDB). *Compare* **ferrimyoglobin**.

ferrimyoglobin *or* **metmyoglobin** (*abbr.*: MetMb) an oxidation product of myoglobin in which its iron atom is in the ferric, Fe(III), state, the sixth coordination valency of which is occupied, in the acid form, by a water molecule, or, in the alkaline form, by a hydroxide ion. Unlike myoglobin, it cannot bind and store dioxygen. The 3D structure is known (Brookhaven file 1MBC.PDB). *Compare* **ferrihemoglobin**.

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ferrioxamine *see* **desferrioxamine**.

ferritin any of a group of electron-dense, major iron-storage proteins that are widely distributed in animal and plant tissues; the iron is stored in a soluble, readily available form. Ferritins consist of a hollow protein shell; the functional molecule, called **apoferritin**, comprises 24 chains and is roughly spherical, with an external diameter of 12.4–13 nm and an internal diameter of 7–8 nm. The central cavity is able to accommodate a core of up to 4500 Fe(III) atoms, mainly as ferric hydroxide-phosphate, $(FeO(OH))_8(FeO{\cdot}PO_4H_2)$. There are two types of ferritin subunits: L (light) and H (heavy); the major chain can be L or H, depending on species and tissue type. In clinical chemistry, low plasma ferritin is an indication of a decrease in the body's iron stores; a concentration of less than 12 $\mu g\ L^{-1}$ indicates a complete absence of stored iron. Examples from human: H chain, database code FRIH_HUMAN, 182 amino acids (21.07 kDa) (3D structure known: database code NRL_1FHA); L chain, database code FRIL_HUMAN, 174 amino acids (19.87 kDa).

ferritin-labelling the use of **ferritin** as an electron-dense label by covalently linking ferritin molecules with the aim of making their position in microscopic specimens apparent by electron microscopy.

ferro+ *comb. form* denoting containing **ferrous** iron.

ferrochelatase EC 4.99.1.1; *systematic name*: protoheme ferro-lyase; *other names*: protoheme ferro-lyase; heme synthetase; an enzyme of the pathway for heme biosynthesis. It catalyses the formation of protoheme from protoporphyrin and Fe^{2+} with release of 2 H^+. Hereditary ferrochelatase deficiency occurs in humans and leads to **porphyria** with accumulation of protopyroxin IX. In bacteria the enzyme is part of **siroheme synthase**. Example (precursor) from human: database code HEMZ_HUMAN.

ferrocytochrome any **cytochrome** in which the iron atom is in the Fe(II) state.

ferroheme *or* (*esp. Brit.*) **ferrohaem** **1 heme**. **2** any Fe(II)–porphyrin coordination complex.

ferrohemochrome any **hemochrome** containing Fe(II).

ferromagnetism the property displayed by certain substances, typically metallic iron, that have a high magnetic susceptibility and that show increasing magnetization with increasing applied magnetic field strength. Some ferromagnetic materials retain their magnetization in the absence of an applied magnetic field, i.e. they become permanent magnets. Ferromagnetism is due to alignment, temporary or permanent, of the spins of the unpaired electrons in domains in the material. —**ferromagnetic** *adj. Compare* **diamagnetism**, **paramagnetism**.

ferroprotoporphyrin *see* **heme**.

ferrous of or containing divalent iron, Fe^{2+} or Fe(II).

ferroxamine *see* **desferrioxamine**.

ferroxidase *see* **ceruloplasmin**.

fertile **1** capable of producing offspring; capable of producing gametes. **2** capable of undergoing growth and development, e.g. fertile seeds or fertile eggs.

fertility the state of being **fertile**.

fertility factor *an alternative name for* **F plasmid**.

fertility vitamin *a former name for* **vitamin E**.

fertilization *or* **fertilisation** **1** the fusion of two gametes of opposite sex to form a zygote. **2** the act or process of fertilizing.

fertilize *or* **fertilise** **1** to provide a female gamete with a male gamete to effect fertilization. **2** to supply soil or water with mineral and/or organic nutrients to assist the growth of plants.

fertilizer *or* **fertiliser** **1** any substance or mixture of substances that is added to soil or water to assist the growth of plants. **2** any object or organism, e.g. an insect, that fertilizes an animal or plant.

fertilizin a mucopolysaccharide from the jelly-coat of the eggs of some species that plays a part in sperm recognition and attracts sperms of the same species.

ferulic acid 4-hydroxy-3-methoxycinnamic acid; 3-(4-hydroxy-3-methoxyphenyl)-2-propenoic acid; an aromatic acid widely distributed in plants. It is a component of **suberin**.

FES/FPS a family of genes encoding nonreceptor tyrosine kinases; v-*fps* is an oncogene of Fujinami-PRCII sarcoma, while v-*fes* is a cognate gene of feline sarcoma virus. FES/FPS proteins contain an SH2 domain (*see* **SH domain**) adjacent to the kinase domain. Overexpression of c-*fes* transforms fibroblasts. Example (human): database code KFES_HUMAN, 822 amino acids (93.47 kDa).

Fe–S protein *abbr. for* iron–sulfur protein.

fet+ *a variant form of* **feto+** (before a vowel).

fetal calf serum *abbr.*: FCS; a serum prepared from the blood of a fetal calf, widely used in tissue culture media.

fetal hemoglobin *an alternative name for* hemoglobin F (*see* **hemoglobin**).

fetal-lung maturity test a test for maturity of the fetal lung based on its content of dipalmitoylphosphatidylcholine (dipalmitoyllecithin). Dipalmitoyllecithin appears in lung surfactant in embryonic life only when the lung reaches maturity. Its concentration in amniotic fluid reflects its production in the lung and can be measured to determine lung maturity as a prenatal test to aid the decision when to induce labour. Formerly, the lecithin/sphingomyelin ratio was measured.

feto+ *or (before a vowel)* **fet+** *comb. form* denoting fetus.

fetomodulin *see* **β-thromboglobulin**.

α-fetoprotein *abbr.*: afp *or* AFP; a protein formed in fetal liver and found in amniotic fluid. In humans, increased levels in the amniotic fluid between the 14th and 17th weeks of gestation reliably predict most cases of anencephaly and spina bifida cystica, and afp determination is performed as an antenatal screening test for such defects. Increased serum levels may be found in adults with hepatoma and teratoma; afp is a valuable marker for liver tumours, blood levels being elevated in about 70% of cases. The normal level in adult human plasma is $<10\ kU\ L^{-1}$, but rises in normal pregnancy. It is similar to **albumin** (serum) and **vitamin D binding protein**. Example (precursor) from human: database code FETA_HUMAN, 609 amino acids (68.60 kDa).

fetuin *see* **α_2-HS-glycoprotein**.

fetus *or* **foetus** the embryo of a mammal in the later stages of development, from the time when the main characteristics of the mature animal can be recognized. In humans the products of conception are termed the fetus from the end of the eighth week of pregnancy until birth. —**fetal** *or* **foetal** *adj.*

Feulgen reaction a specific cytochemical reaction to indicate the presence of DNA. It is based on converting DNA, but not RNA, to apurinic acid by acid hydrolysis with release of the aldehyde functions; the aldehyde functions then give a magenta colour on treatment of the specimen with **Schiff reagent**. Tissue giving such a reaction is termed **Feulgen positive**, whereas the absence of such a reaction characterizes **Feulgen-negative** tissues. The reaction is not suitable for living cells. [After Robert Joachim Feulgen (1884–1955), German chemist.]

FFA *abbr. for* free fatty acid(s). *Compare* **NEFA**.

F factor *an alternative name for* **F plasmid**.

F′ factor *an alternative name for* **F′ plasmid**.

F_0F_1 complex *see* **H⁺-transporting ATP synthase**.

(F_1 + F_2) fragment *see* **heavy meromyosin**.

F_1 fragment the separated globular head portion of a **myosin** molecule.

F_2 fragment the separated fibrous part of **heavy meromyosin**.

F_3 fragment *see* **light meromyosin**.

FGAM synthase *see* **phosphoribosylformylglycinamidine synthase**.

FGAR *abbr. for* formylglycinamide ribonucleotide; an intermediate in **purine biosynthesis**.

FGF *abbr. for* fibroblast growth factor.

FGR a gene encoding a nonreceptor tyrosine kinase and belonging to the ***src*** family; v-*fgr* is the oncogene of the feline sarcoma virus Gardner-Rasheed. *FGR* transforms most mammalian

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fibroblasts, but not epithelial cells. Example of expressed protein from human: database code KFGR_HUMAN.

FH_2 *abbr. (not recommended) for* dihydrofolate or dihydrofolic acid.

FH_4 *abbr. (not recommended) for* tetrahydrofolate or tetrahydrofolic acid.

FIA *abbr. for* fluorescence immunoassay.

fiber *the US spelling of* **fibre**.

fibre *or (US)* **fiber** any natural filamentous structure, typically pliable and often strong; by extension the term is applied to filamentous glass or filamentous synthetic polymeric materials. —**fibrous** *adj.*

fibre diagram the X-ray diffraction pattern obtained from a stretched, hence orientated, sample of an amorphous, solid, naturally occurring or synthetic fibrous linear polymer when analysed by the rotating crystal method.

fibre optics **1** a flexible glass or plastic fibre, or a bundle of such fibres, used as a light guide for the transmission of light, especially as images or digitized information. **2** the study of the optical properties of transparent fibres.

fibriform having the form of a fibre or fibres.

fibril any small thread or fibre, bundles of which may constitute a fibre. —**fibrillar, fibrilliform** *adj.*

fibrillar collagen *see* **collagen**.

fibrillarin a component of a nucleolar small nuclear ribonucleoprotein particle (snRNP) thought to participate in the first step in processing pre-rRNA and associated with U3, U8, and U13 snRNP RNAs. It is the nucleolar scleroderma antigen, rich in N^G,N^G-dimethylarginine and common to the major family of nucleolar snRNPs. Example from human: database code FBRL_HUMAN, 321 amino acids (33.78 kDa).

fibrillin a large glycoprotein isolated from fibroblast cell cultures. It is a structural Ca^{2+}-binding component of connective tissue microfibrils, and contains 34 six-cysteine (EGF-like) repeats and five eight-cysteine (TGF-β1 binding protein-like) repeats. Defects are associated with the autosomal dominant disorder, Marfan's syndrome. Example (fibrillin 1 precursor) from human: 2871 amino acids (311.96 kDa).

β-fibrillosis *see* **amyloidosis**.

fibrin the product(s) formed from **fibrinogen** when blood plasma clots. The initial stage of this process is the formation of a **fibrin monomer** (≈340 kDa) through the action of **thrombin**, which cleaves negatively charged **fibrinopeptides** A and B from fibrinogen. In intact fibrinogen, fibrinopeptides A and B prevent self-association of fibrinogen. Their removal enables the resultant molecule to self-associate readily in a staggered side-by-side arrangement, forming the fibrous **soluble fibrin polymer**. This in turn is converted into **insoluble fibrin polymer** (*see* **desmofibrin**) through the action of plasma transglutaminase (factor XIIIa, EC 2.3.2.13) which, in the presence of calcium ions, creates covalent cross-links between the monomers by transamidating glutamine residues with the amino groups of the side chains of lysine residues in other monomers. *See also* **blood coagulation**.

fibrinase *an alternative name for* **plasmin**.

fibrin monomer *see* **fibrin**.

fibrinogen *or* **factor I** a highly soluble, 340 kDa, elongated protein of blood plasma concerned in clot formation. It is converted into **fibrin** monomer by the action of **thrombin**. Fibrinogen is a hexamer, 46 nm long and 9 nm maximal diameter, containing two sets of three nonidentical chains (α, β, and γ), linked to each other by disulfide bonds. The N termini of all chains are contained in a central nodule, diverging from which are two three-chain coiled coils; these connect the central nodule to the distal nodules containing the distal domains; there are long C termini of the α chains. Thrombin cleaves four Arg–Gly bonds, releasing two each of **fibrinopeptides** A and B from the α and β chains, and forming fibrin monomer (the intact chains in fibrinogen being referred to as the Aα and Bβ chains). This exposes the N-terminal polymerization sites responsible for the formation of the soft clot, which is converted into the hard clot by **factor XIIIa**. This catalyses the ε-(γ-glutamyl)lysine cross-linking between γ chains (stronger) and between α chains (weaker) of different monomers. Fibrinogen also acts as a cofactor in platelet aggregation (a binding site on the γ chain participates). Example sequences (precursors, human): α, database code FIBA_HUMAN, 644 amino acids (69.68 kDa); β, database code FIBB_HUMAN, 491 amino acids (55.87 kDa); γ-A, database code FIBG_HUMAN, 437 amino acids (49.43 kDa); an alternative (γ-B or γ′) is produced by differential splicing; database code FIBH_HUMAN, 453 amino acids (51.44 kDa). *See also* **blood coagulation**.

fibrinogenase *an alternative name for* **thrombin**.

fibrinolysin *an alternative name for* **plasmin**.

fibrinolysis the process of the dissolution of fibrin in blood clots resulting from the proteolytic action of **plasmin** or other enzymes, e.g. **streptokinase** or the proteases in snake venom. —**fibrinolytic** *adj.*

fibrinopeptide either of the types of negatively charged peptide cleaved off **fibrinogen** when it is converted to **fibrin** by the action of **thrombin**. Human **fibrinopeptide A** is a 16-residue peptide cleaved from each of the fibrinogen Aα chains; structure (human): ADSGEGDFLAEGGGVR; **fibrinopeptide B** is a 14-residue peptide cleaved from each of the Bβ chains.

fibrin polymer *see* **fibrin**.

fibrin stabilizing factor *or* **fibrin stabilising factor** *abbr.*: FSF; *an alternative name for* factor XIIIa; *see* **blood coagulation**.

fibroblast *or* **fibrocyte** a flattened, irregular, branched, motile cell found distributed throughout vertebrate connective tissue. Such cells form, secrete, and maintain the extracellular collagen and mucopolysaccharide of this tissue. Similar cells occur in many invertebrates.

fibroblast growth factor *abbr.*: FGF; any of various growth factors with strong mitogenic potential, characterized by their high affinity for heparin; they are mitogenic for mesodermal and neuroectodermal cells but not for endodermally derived cells. Two major subtypes are recognized, based on their ease of elution from heparin columns: an acidic group (aFGFs), and a less-easily eluted basic group (bFGFs). FGFs have angiogenic properties, may function as inductive agents during embryonic development, and are useful as a partial or total substitute for serum in tissue culture. Those of the acidic group have been isolated mainly from brain or retina; they include acidic brain fibroblast growth factor (brain aFGF), astroglial growth factor-1 (AGF-1), retina-derived growth factor (RDGF), eye-derived growth factor-2 (EDGF-2), endothelial cell growth factor (ECGF), and heparin-binding growth factor (HGFα and HGFβ). Those of the basic group have been isolated from brain, retina, and cartilage; they include basic brain fibroblast growth factor (brain bFGF), eye-derived growth factor-1 (EDGF-1), astroglial growth factor-2 (AGF-2), and cartilage-derived growth factor (CDGF). Example, basic fibroblast growth factor (human): database code NRL_2FGF, 126 amino acids (14.41 kDa); 3-D structure known (beta barrel). FGF-3, so named because aFGF and bFGF had already been identified, a monomer of 239 amino acids, is expressed during embryonic development and by mammary tumour epithelial cells; it is the product of the *int-2* oncogene, and has properties similar to those of basic FGFs. FGF-4 is the product of the *hst*/KS3 gene, comprises 205 amino acids, is expressed during development and by some tumours, is mitogenic for fibroblasts and endothelial cells, and is angiogenic *in vivo*. FGF-5 (identified by DNA probes in human bladder carcinoma, hepatoma, and endometrial carcinoma) is a monomer of 267 amino acids; it is expressed by fibroblasts, epithelium, some tumour cells, and during embryonic development, and is mitogenic for fibroblasts and endothelial cells. FGF-6 is the product of *hst-2* (identified by a screen for *hst*-related genes) and is a monomer of 208 amino acids; it is expressed during embryonic development and in adult testis, heart, and skeletal muscle, and is mitogenic for fibroblasts but only weakly for endothelial cells. FGF-7 (ker-

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atinocyte growth factor) is a monomer of 194 amino acids; it is expressed by epithelial tissue and is mitogenic for epithelial cells but not for fibroblasts or endothelial cells. *See also* ***KS/hst***.

fibroblast growth factor receptor *abbr.*: FGFR; any of the plasma membrane **tyrosine kinase** proteins that bind **fibroblast growth factors** and mediate their intracellular effects. All have a single transmembrane helical domain of 21 amino acids, an extracellular domain of about 350 amino acids with three immunoglobulin domains (but variants with fewer are known), and a cytoplasmic domain of about 410–425 amino acids within which is a tyrosine kinase domain which is activated by ligand binding. Six to nine potential N-linked glycosylation sites are present in the extracellular domain. FGFRs are classified into five types. FGFR1 was isolated as a partial cDNA clone encoding an *fms*-like gene (*flg*) and is also known as flg. Common variants have only two immunoglobulin (Ig) domains. Example from *Rattus norvegicus* (precursor): database code FGR1_RAT, 822 amino acids (91.82 kDa). FGFR2 was isolated as a tyrosine kinase gene encoding a bacterial expressed kinase (***bek***). Common variants of this also have deletion of the first Ig domain. Example from *Xenopus laevis* (precursor): database code FGR2_XENLA, 813 amino acids (91.34 kDa). FGFR3 is the product of *cek2* (*see* **cek**); example, human (precursor): FGR3_HUMAN, 806 amino acids (87.71 kDa). FGFR4 was isolated as a clone from human erythroleukemia cells; example, human (precursor): database code FGR4_HUMAN, 802 amino acids (87.94 kDa). A fifth type of FGFR is known as flg-2. FGFR1 and 2 are expressed by a variety of species, tissues, and cell lines, but FGFR3, FGFR4 and flg-2 have been isolated from a limited number of sources. Heparan sulfate proteoglycans promote binding of FGFs to FGFRs. Binding of ligand to the extracellular domain of FGFRs induces oligomerization of receptors, autophosphorylation, and phosphorylation of intracellular proteins that associate with the activated receptor through their SH2 domains (*see* **SH domain**). Prominent among these is phospholipase Cγ1 (*see* **phospholipase**).

fibroblast surface antigen *a variant form of* surface fibroblast antigen; *see* **fibronectin**.

fibrocyte *an alternative name for* **fibroblast**.

fibroglycan *see* **syndecan-2**.

fibroin *or* **silk fibroin** the protein of the silk fibres that are secreted by the posterior gland of the larva of the silk moth, *Bombyx mori*. It comprises two chains, heavy and light, linked by disulfide bond(s). Both heavy and light chains assembled as a mature protein are needed for efficient intracellular transport and secretion of fibroin; the secondary structure is largely beta sheet. Example (light chain) from *B. mori*: database code FBOL_BOMMO, 262 amino acids (27.64 kDa).

fibronectin any of a group of related adhesive glycoproteins of high molecular mass found on the surface of animal cells, in connective tissue matrices, and in extracellular fluids. They bind to cell surfaces, collagen, fibrin, heparin, DNA, actin, etc. and are involved in cell adhesion, cell motility, opsonization, wound healing, and maintenance of cell shape. Fibronectin is a disulfide-bonded heterodimer. Fibronectins can be classified into two immunologically cross-reacting groups: **plasma fibronectins** (*also called* cold-insoluble globulin *or* cell attachment protein *or* cell adhesion factor *or* cell spreading factor *or* anti-gelatin factor *or* opsonic α_2-SB-glycoprotein); and **cellular fibronectins** (*also called* cell surface protein *or* large external transformation sensitive (LETS) protein *or* surface fibroblast antigen *or* galactoprotein A *or* zeta protein). Cellular fibronectin (which is the major cell surface protein of cultured fibroblasts) is greatly reduced or even lost when a variety of cell types are transformed by oncogenic viruses, chemical carcinogens, or temperature-sensitive viruses at the permissive temperature and several of the morphological changes associated with transformation can be partially reversed by addition of appropriate amounts of purified cellular fibronectin. There are three types of fibronectin domain (I, II, III) with several versions in the same protein; extra domains and a connecting strand 3 are present in some forms of fibronectin and absent in others; these differences are due to alternative splicing. Human (precursor): database code FINC_HUMAN, 2386 amino acids (262.39 kDa). Fibronectin binds to **integrins** $\alpha_4\beta_1$, $\alpha_v\beta_1$, $\alpha_v\beta_3$, $\alpha_v\beta_5$, $\alpha_v\beta_6$, and $\alpha_4\beta_7$. [From Latin *fibra*, fibre and *necto*, to attach.]

fibrosome an artificial macromolecular complex of fibronectin layered on an agar-coated substrate.

fibrous protein any protein able to aggregate into fibres or filaments and serving mainly as a structural protein. The polypeptide chains in such proteins are either extended or coiled in one dimension and their structure is maintained largely by interchain hydrogen bonds.

fibulin a Ca^{2+}-binding glycoprotein of the extracellular matrix with nine EGF-like repeats. Four forms (A–D) differ only in their C-terminal region and arise by alternative splicing. Example, isoform A precursor from human: database code FBLA_HUMAN, 566 amino acids (61.53 kDa).

ficain *or* **ficin** a cysteine endopeptidase, EC 3.4.22.3, from *Ficus* spp. with preferential cleavage at Lys-, Ala-, Tyr-, Gly-, Asn-, Leu-, and Val-. The name is also used for the crude dried latex from *Ficus* spp., but extracts of only a small proportion of these (in one study only 13 out of 43 species) contain proteolytic activity. Its action is similar to that of **papain**.

ficin *another name for* **ficain**.

Fick's first diffusion law a mathematical description of the physical process of solute diffusion; the flux (mass transferred) of particles, J, diffusing across a unit plane in unit time is given by:

$$J = -D(\partial c/\partial x),$$

where the mass concentration gradient at x is $\partial c/\partial x$ and D is the **diffusion coefficient** for the solute. [After Adolph Eugen Fick (1829–1901), German physiologist.]

Fick's second diffusion law a mathematical description of the rate of change in mass concentration, c, at point x of the diffusing particles with time, $(\partial c/\partial t)$, during solute diffusion, for unsteady conditions $(\partial c/\partial x \neq 0)$; it is given by:

$$(\partial c/\partial t) = D(\partial^2 c/\partial x^2),$$

where D is the **diffusion coefficient**, assumed to be independent of the concentration.

Fick unit *symbol*: F; a non-SI unit sometimes used to express a **diffusion coefficient**; it is equal to 10^{-7} cm^2 s^{-1}.

ficolin a multimeric protein so named because of its fibrinogen- and collagen-like domains; it was originally isolated as a TGF-β1 binding protein. Recombinant ficolin-α and ficolin-β expressed from cDNA do not bind TGF-β1. Ficolin-α is expressed preferentially in uterus, lung, and placenta whereas ficolin-β RNA is most abundant in skeletal muscle. The function is at present unknown. Example, ficolin-α from pig: database code A47172, 323 amino acids (34.64 kDa).

Ficoll *or* **Ficoll 400** a synthetic copolymer of sucrose and epichlorhydrin. It has a branched structure, a high content of hydroxyl groups, which renders it very water-soluble (up to 50% w/v), and a mass average M_r of 400 000 ± 100 000. Solutions of Ficoll have low osmotic pressures and are useful in preparing density gradients; Ficoll is widely used in preparing continuous or discontinuous gradients for separating cell types. Ficoll 70, with an M_r of 70 000, is useful in perfusion studies.

Ficoll-Paque *the proprietary name for* an aqueous solution of **Ficoll** and diatrizoate sodium with a density of 1.077 ± 0.001 g cm^{-3}. It is useful for the one-step separation of lymphocytes from a sample of anticoagulant-treated blood and for the preparation of other cell types by density-gradient centrifugation.

fidelity the degree to which the output of any system accurately describes or reflects the input to the system. The term is used

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especially of the processes of replication, translation, and transcription, and of electronic amplifiers.

field 1 a region of space in which a force is exerted on an object because of its charge (**electric field**), magnetic dipole (**magnetic field**), mass (**gravitational field**), or other attribute. 2 a region of space through which (ionizing) radiation is passing. 3 *or* **field of view** the area within which an object is observable with a microscope or other optical instrument.

Fieser's solution a solution for removing dioxygen from any other nonacidic, nonoxidizing gas. It contains potassium hydroxide, anthraquinone β-sulfonate, and sodium thiosulfate. Red when fresh, it becomes colourless when exhausted. [After Louis Frederick Fieser (1899–1977), US chemist.]

FIGLU *abbr. for* formiminoglutamate.

figure of merit the square of the efficiency divided by the background count for a given liquid scintillation system (*see* **liquid-scintillation counting**). It is useful for optimizing the scintillator composition and the discriminator settings for the counting channel(s).

filaggrin a protein that aggregates keratin intermediate filaments and promotes disulfide-bond formation amongst them during terminal differentiation of mammalian epidermis. It is initially synthesized as a large, insoluble, highly phosphorylated precursor containing many tandem copies of 324 amino acids, which are not separated by 'large linker' amino-acid sequences. The precursor is deposited as keratohyalin granules; during terminal differentiation it is dephosphorylated and proteolytically cleaved. Example from human (partial sequence): database code FILA_HUMAN, 416 amino acids (44.06 kDa).

filament any very thin, threadlike structure. *See also* **actin**, **microfilament**, **thick filament**, **thin filament**. —**filamentary** *or* **filamentous** *adj.*

filamin a protein, extractable from smooth muscle and other tissues, that induces a calcium-ion-insensitive gelation of actin. It promotes orthogonal branching of actin filaments and links actin filaments to membrane glycoproteins. It exists as a homodimer and contains an **actin-binding domain**. Example, nonmuscle filamin (human): database code ABP2_HUMAN, 2647 amino acids (280.45 kDa).

filensin a membrane- and cytoskeleton-associated protein. It is an intermediate filament type III unique to lens fibre cells. It has primary and secondary structural similarity to other intermediate filament proteins and serves as an anchorage site for ***vimentin*** intermediate filaments. Example (bovine): database code S32103, 755 amino acids (82.86 kDa).

filial generation *symbol*: F; any of the generations of living organisms following a particular parental generation. The generation resulting from a mating of the parents is the **first filial generation** *symbol*: (F_1), while that resulting from crossing of F_1 individuals is the **second filial generation** *symbol*: (F_2), and so on.

filipin a neutral polyene antibiotic from *Streptomyces filipinensis*. It is similar in action to **amphotericin B**.

film badge a masked photographic film worn by workers exposed to ionizing radiation to indicate the extent of their exposure to radiation.

filter 1 any piece or layer of material used or useful for (completely or partially) removing selected components, especially in suspension, from liquid or gaseous mixtures, e.g. a sheet of paper, a stratum of sand (or similar material), or a piece of porous ceramic or plastic. *See also* **membrane filter**, **ultrafilter**. 2 a device incorporating such a piece or layer of material. 3 a block or sheet of material for reducing the intensity of particulate radiation. 4 a screen for selectively absorbing or attenuating electromagnetic radiation or sound waves of some particular or all frequencies. 5 a passive electronic circuit or device that selectively attenuates or allows the passage of certain frequencies of an electrical signal. 6 to remove or separate (suspended particles, macromolecular solutes, selected frequencies of electrical signal or electromagnetic radiation, etc.) from (a heterogeneous or composite fluid, beam, signal, etc.) by means of a filter; to pass (something) through a filter. 7 *(as modifier)* containing or using a filter or filters, or used for filtering, as in a filter fluorometer or filter photometer.

filterable *or* **filtrable** capable of being filtered; able to pass through a (specified) filter.

filterable agent *a former name for* bacteriophage, virus, or other submicroscopic noncellular microorganism.

filterable virus *a former name for* a virus the particles of which are capable of passing through a filter that will retain bacteria and other cellular microorganisms.

filter membrane *an alternative term for* **membrane filter**.

filter paper porous, unsized paper used for filtration; a disk, piece, or sheet of such paper. Such paper may be chemically treated for special applications, e.g. for use in quantitative analysis; it is also used in **paper chromatography**.

filter press a device for effecting filtration, consisting of a series of (metal, plastic, or wooden) frames the two sides of which are covered with filter cloth. The frames are clamped together and the liquid to be filtered is pumped into them in such a way that the solid residue forms a cake between the cloths and the liquid filtrate is conducted away separately.

filter pump a type of vacuum pump used to assist filtration, in which a jet of water forced through a narrow orifice entraps air from the system being evacuated.

filtrable *a variant spelling of* **filterable**.

filtrate the liquid or gas that has passed through a **filter** (def. 1).

filtration the act or process of separating or (completely or partially) removing selected components (of a mixture) by means of a **filter** (def. 1), to produce a **filtrate**. The term includes **gel filtration**, **membrane filtration**, and **ultrafiltration**.

filtration enrichment a method for isolating fungal auxotrophs. Mutagenized spores are placed in a minimal medium in which only normal spores germinate and produce a mycelial network. This mycelial network is then removed by filtration and the remaining auxotrophic spores are provided with an enriched medium to allow their germination, growth, and propagation.

filtration fraction *(in physiology)* the fraction of the plasma that is filtered through the renal glomeruli. It is equal to the **glomerular filtration rate** divided by the renal plasma flow and is frequently taken to be equal to the ratio of the inulin clearance to *p*-aminohippurate clearance.

fimbria (*pl.* **fimbriae**) 1 *(in botany and zoology)* a fringe or fringelike edge or margin, e.g. especially at the opening of a fallopian tube. 2 *(in bacteriology) an alternative term for* **pilus** (especially a common pilus). —**fimbrial** *adj.*

fimbriate *or* **fimbriated** characterized by or possessing fimbriae; fringed at the edge or margin.

fimbrin an **actin-binding protein** involved in the development and maintenance of cell polarity. Example from *Saccharomyces cerevisiae*: database code FIMB_YEAST, 642 amino acids (71.69 kDa).

fine structure *or* ***microstructure*** any structural detail observable in genetic material, microscopic specimens, spectra, etc. when examined at high magnification or resolution. *See also* **hyperfine structure**.

fingerprinting any pattern obtained by a variety of means that is characteristic of a biological entity, including 1 the electrophoretic or chromatographic pattern obtained after a process in which a protein is digested, usually enzymically, in defined conditions to produce a mixture of peptides, the nature of the mixture being dependent on the particular protein and the conditions of digestion. The distribution pattern of spots is rarely, if ever, duplicated if a different protein is used. 2 a set of one or more amino-acid **motifs** (def. 2) obtained by aligning conserved regions of proteins found in protein sequence databases to provide a sequence or set of sequences characteristic of a particular function e.g. the rat metabotropic glutamate receptor 2 precursor fingerprint has seven motifs, the first of which is the 22-residue

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VGPVTIACLGALATLFVTVIFI.

The technique involves alignment followed by maximization of sequence information through iterative scanning, with multiple motifs, of a large composite database. The results are held in the ***PRINTS*** database. *See also* **Appendix E. 3** the result of **genetic profiling**.

firefly lantern *or* **lantern** the luminescent abdominal organ, or photophore, of the American firefly, *Photinus pyralis*, a common source of the enzyme **luciferase** and its luminogenic substrate **luciferin**.

firefly luciferase *see* **luciferase**.

firefly luciferin *see* **luciferin**.

first law of photochemistry *an alternative name for* **Grotthus and Draper law**.

first law of thermodynamics *see* **thermodynamics**.

first messenger *an alternative term* sometimes used for **hormone** to distinguish it from **second messenger**. *See also* **chemical messenger**, **pheromone**.

first-order kinetics the kinetics of a first-order reaction; *see* **order of reaction**.

first-order reaction *see* **order of reaction**.

first-pass clearance *or* **first-pass elimination** *or* **first-pass metabolism** the effect of passage of a drug administered by mouth through the liver before it reaches the systemic circulation. Some drugs, in spite of their rapid uptake through the gut mucosal membrane, appear in low concentration in the systemic circulation and hence more has to be administered by mouth than by intravenous injection. As little as 10–20% of the drug may reach the systemic circulation unchanged as a result of their metabolism, mainly by the liver. Some authors extend the term to include metabolism also by the cells of the gut mucosal membrane.

Fischer **1 Edmond Henri** (1920–), Swiss-born biochemist; Nobel Laureate in Physiology or Medicine (1992) jointly with E. G. Krebs 'for their discoveries concerning reversible protein phosphorylation as a biological regulatory mechanism'. **2 Emil Hermann** (1852–1919), father of H. O. L. Fischer (*see* def. 5), German organic chemist, stereochemist, enzymologist, and one of the most famous chemists of the nineteenth century, renowned in particular for his synthetic work on dyes, for elucidating the structures of and synthesizing a wide range of natural products (including sugars, purines, amino acids, and polypeptides), for establishing the steric configurations of all the aldohexoses and aldopentoses (*see also* **Fischer convention**), and for recognizing the stereochemical specificity of enzyme action (*see* **lock-and-key model**); Nobel Laureate in Chemistry (1902) 'in recognition of the extraordinary services he has rendered by his work on sugar and purine syntheses'. **3 Ernst Otto** (1918–), German inorganic chemist; Nobel Laureate in Chemistry (1973), the prize being shared with G. Wilkinson 'for their pioneering work, performed independently, on the chemistry of the organometallic, so called sandwich compounds'. **4 Hans** (1881–1945), German organic chemist noted for his structural and synthetic work on various linear or macrocyclic tetrapyrroles; Nobel Laureate in Chemistry (1930) 'for his researches into the constitution of haemin and chlorophyll and especially for his synthesis of haemin'. **5 Hermann Otto Laurenz** (1888–1960), son of Emil H. Fischer (*see* def. 2), German organic chemist and biochemist noted particularly for his unequivocal chemical syntheses (with E. Baer) of glyceraldehyde 3-phosphate and glycerone phosphate.

Fischer conventions conventions used in the construction of plane projection formulas and first formulated by E. H. Fischer (*see* **Fischer** def. 2). The first convention may be stated as 'All of the tetrahedral apices that connect asymmetric carbon atoms lie in a straight line in the plane of the paper. This line shall contain the lower edges of all these tetrahedra, their other apices being above the plane and on opposite sides of the line' (*see* **Fischer projection**). The second convention is the assumption of one specified configuration for (+)saccharic acid and hence for glucose. At the time of Fischer's work, absolute configurations were not known. Fortunately, he guessed the correct configuration for (+)glucose (now designated D-glucose).

Fischer ester *former name for* glyceraldehyde 3-phosphate (*see* **D-glyceraldehyde 3-phosphate**). [After H. O. L. Fischer (*see* **Fischer** def. 5).]

Fischer projection a diagrammatic representation in two dimensions (as on paper) of the three-dimensional structure of an open-chain chiral molecule of the type R^1CHXR^2, useful particularly for monosaccharides (X = OH) and their derivatives and for amino acids (X = NH_2) and their derivatives. According to the first **Fischer convention**, the carbon chain is written vertically with the most highly oxidized carbon atom (number 1) at the top, the bonds between the carbon atoms being either in or below the plane of the paper; the hydrogen atoms and the X groups, written to the left and right of the carbon atoms to which they are attached, are considered as being in front of the plane of the paper. If X is on the right, the configuration at that carbon atom is designated by the prefix D- (from Latin *dexter*, turned to the right), whereas if X is on the left, the configuration is designated L- (from Latin *laevus*, turned to the left). *See also* **D/L convention**.

FISH *abbr. for* fluorescence *in situ* hybridization.

fish-odour syndrome a condition of humans characterized by an offensive odour of rotting fish, due to abnormal excretion of trimethylamine in the breath, urine, sweat, saliva, and vaginal secretions, especially after eating foods containing trimethylamine (e.g. sea fish) or choline. It results from a reduced ability to oxidize trimethylamine *N*-oxide, normally effected by liver microsomal monooxygenases.

fish oil oil obtained from the liver or flesh of fish; it is comparatively rich in fatty acids of the *n*-3 family (*see* **fatty-acid nomenclature**). Generally, the flesh of so-called oily fish, such as herring, mackerel, salmon, and trout, has a higher content of C_{20} and C_{22} *n*-3 acids than that of white fish such as cod or plaice. Recently, increasing the dietary content of long-chain *n*-3 fatty acids has been promoted as a prophylactic measure in the prevention of heart disease, though the mechanisms suggested are conjectural. *See also* **cod-liver oil**.

Fiske and SubbaRow method a colorimetric method for determination of inorganic phosphate, based on the production of a blue colour when the sample is treated with ammonium molybdate and 1-amino-2-naphthol-4-sulfonic acid. [After Cyrus Hartwell Fiske (1890–1978) and Yellapragrada SubbaRow (1896–1948).]

FISP-12 *another name for* mouse **connective tissue growth factor**.

fissile tending to undergo **fission**.

fission **1** *or* **nuclear fission** *(in physics)* a nuclear reaction in which a heavy atomic nucleus splits into two (or, rarely, three or four) approximately equally sized nuclides, with release of a considerable amount of energy. **2** *(in biology)* cleavage of cells or division of unicellular organisms into two (or more) parts.

fission product any of the stable or unstable nuclides resulting from **fission** (def. 1).

FITC *abbr. for* **1** fluorescein isothiocyanate. **2** the fluorescein isothiocarbamoyl group.

fitness *(in biology)* the survival value and the reproductive capability of a given genotype as compared with the average of the population or of other genotypes in the population.

fix **1** to render, or to become, stable, firm, or insoluble; to attach (to something). **2** *(in chemistry)* to convert a free element into one of its compounds; especially to convert atmospheric dinitrogen into nitrogen-containing substances (*see* **nitrogen fixation**); to convert a volatile or fluid substance into a non-volatile or solid form; to combine an inorganic substance with an organic substance. **3** *(in biology)* to preserve (and harden) cells, tissues, or organisms for subsequent (microscopic) study. **4** *(in photography)* to treat a film or plate with fixer so as to render permanent the developed image. —**fixation** *n.*

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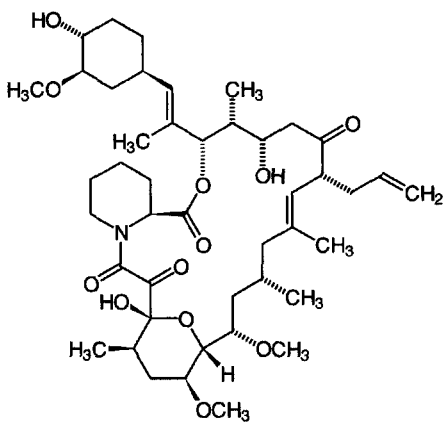
fixative a protein-denaturing fluid, e.g. formaldehyde, that is used to **fix** (def. 3) biological material for (microscopic) study.

fixed antibody *see* **cell-bound antibody**. *Compare* **humoral antibody**.

fixed nitrogen any product of **nitrogen fixation**.

fixer *(in photography)* a chemical solution used to remove unexposed, hence unreduced, silver halide granules from a photographic emulsion after the image has been developed.

FK506 an immunosuppressant, isolated from *Streptomyces tsukubaensis*. It is a member of the macrolide antibiotic family, has an M_r of 803, and binds to the **FKBP**-binding proteins. It is a potent inhibitor of T-cell activation and prevents allograft rejection. The *in vivo* function of this **immunophilin** is not clear but in a complex with FKBP it blocks the action of **calcineurin** in the liver. It is also a powerful neuroprotective agent in an *in vivo* model of focal cerebral ischemia and may have clinical potential for the treatment of stroke. FK506 also reduces **nitric oxide** production by inhibiting the calcineurin-mediated dephosphorylation of **nitric-oxide synthase** (EC 1.14.13.39). One proprietary name is Tacrolimus.



FKBP *abbr. for* FK506-binding protein; any of an extensive family of small proteins to which the immunosuppressant **FK506** binds. They are found in many species from bacteria to humans. Like **cyclophilin** they possess **peptidyl-prolyl isomerase** activity (EC 5.2.1.8), but have no similarity in structure. Both types belong to the class of proteins termed **immunophilins**. Example from *Drosophila melanogaster:* database code FKBP_DROME, 108 amino acids (11.6 kDa).

flagella *the plural of* **flagellum**.

flagellate **1** describing unicellular organisms that have a **flagellum** or flagella. **2** resembling a flagellum. **3** an organism that propels itself by means of a flagellum or flagella, especially any member of the protozoan superclass Mastigophora.

flagellin any member of a group of similar monomeric soluble globular proteins that constitute the subunits of bacterial flagella. They also comprise the major antigens of several bacteria, including *Salmonella* spp., which alternate between the production of two antigenic forms of flagella, termed phase 1 and phase 2. Example, phase-1 flagellin from *S. typhimurium* SL877: database code STYFLGH1I, 490 amino acids (51.28 kDa); there are three flagellin motifs.

flagellum (*pl.* **flagella** *or* **flagellums**) **1** the specialized locomotory appendage of bacteria of certain taxonomic groups, consisting of a noncontractile, filiform extension through the cell surface, borne singly, in groups, or as a covering layer. It is commonly 3–20 μm long and 12–25 nm in diameter, is built up of several (often three) longitudinally arranged chains of **flagellin** subunits (often in a spiral), and is anchored to the cell envelope by a **basal body** (def. 1), which imparts rotatory motion to it. Bacterial flagella carry the H (or flagellar) antigens, which are useful in some instances, e.g. in *Salmonella* spp., for classification. **2** the specialized locomotory appendage of the motile cells of unicellular eukaryotes of certain taxonomic groups (e.g. some algae and protozoa) and also of the male gametes (spermatozoa) of most groups of animals. Usually borne singly or in small groups, it is a whiplike structure, similar to, but generally longer than a **cilium**, commonly about 40 μm long and 200–300 nm in diameter. It is built up of an outer membranous sheath, which is a continuation of the cell membrane, and an inner **axoneme**, which terminates within the cell at a **basal body** (def. 2). Eukaryotic flagella often exhibit undulatory motion, which in multiflagellate organisms can occur as coordinated beating. —**flagellar** *adj.*

flame emission spectrophotometry a type of **atomic emission spectrophotometry** in which excitation is produced by a flame.

flame ionization detector *or* **flame ionisation detector** a sensitive detector used in **gas chromatography** that depends on changes in the electrical conductivity of a flame (burning a mixture of dihydrogen and dinitrogen in air or dihydrogen and dioxygen), brought about by ionization of the vapours of organic substances emerging from the column.

flame photometer an instrument for **flame photometry**.

flame photometry an earlier and simpler, often direct-reading, version of atomic **emission spectrophotometry** in which isolation of the required emission line(s) is achieved by the use of an appropriate filter.

flame spectrophotometry any form of **atomic absorption spectrophotometry** or atomic **emission spectrophotometry** in which excitation is produced by a flame.

flanking marker (DNA) a DNA marker on either side of a locus; a DNA sequence on either side of a gene.

flash evaporation a technique for concentrating a solution at a relatively low temperature thus preventing denaturation of nonvolatile solutes. The solution is placed in a round-bottomed flask or other vessel, which is then rapidly rotated and evacuated; the vapour removed from the solution is reliquefied in a condenser and retained in a cold trap. The rotation of the vessel causes the liquid to form a comparatively thin film, which increases its surface-to-volume ratio, thereby assisting evaporation.

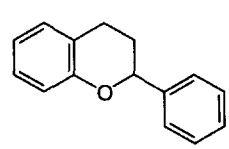
flash evaporator an apparatus for **flash evaporation**.

flash photolysis a technique for investigating short-lived primary or subsequent intermediates, e.g. radicals, in a **photochemical reaction**. The sample is subjected to a brief but powerful flash of light of appropriate wavelength and the **photolysis** products are identified by their absorption or fluorescence spectra, using an independent source of radiation. The kinetics of very fast reactions can be investigated by this technique.

flash point the lowest temperature at which the vapour above a volatile combustible substance will ignite to produce a momentary flash when a small flame is applied under specified conditions.

flat-bed indicating that a technique is carried out in a horizontal plane, e.g. flat-bed chromatography.

flavan 2-phenylchroman; 2,3-dihydro-2-phenylbenzopyran; the parent ring structure on which the structures of flavanols, flavanones, flavones, flavonols, and other classes of aglycons of flavonoids are based.



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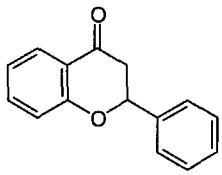
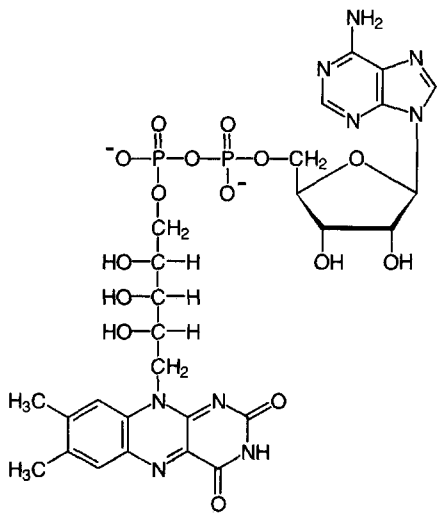
flavanol any hydroxylated derivative of **flavan**. Glycosides of flavan-3-ol and of flavan-3,4-diol respectively form two of the classes of **flavonoid** (def. 1).

flavanone **1** 2,3-dihydroflavone; 2-phenylchroman-4-one; 2,3-dihydro-2-phenylbenzopyran-4-one; it is the 4-oxo derivative of **flavan** and the 2,3-dihydro derivative of **flavone**. **2** any of a group of hydroxylated derivatives of flavanone. Flavanone glycosides are colourless; they are found in flowering plants and form one of the classes of **flavonoid** (def. 1).



flavin *or (formerly)* **flavine** *the stem name and trivial name for* any member of a group of yellow-coloured, 10-substituted derivatives of 7,8-dimethylisoalloxazine, as in **riboflavin**, **flavin-adenine dinucleotide**, etc.

flavin-adenine dinucleotide *abbr.*: FAD; adenosine diphosphate riboflavin; adenosine(5′)diphospho(5′)riboflavin; riboflavin 5′-(adenosine 5′-diphosphate); 7,8-dimethyl-10-[5-(adenosine(5′)diphospho)-D-ribityl]isoalloxazine; an atypical dinucleotide, not only in that it contains, as does **nicotinamide-adenine dinucleotide**, a phosphoric anhydride linkage between the component mononucleotide units, which in this instance are **adenosine 5′-phosphate** and **flavin mononucleotide**, but also because the latter is not strictly a nucleotide in any case, although considered as one (*see* **nucleotide** (def. 3)). It forms the coenzyme or the prosthetic group of various flavoprotein oxidoreductase enzymes, in which it functions as an electron acceptor by being reversibly converted to **flavin-adenine dinucleotide (reduced)**. *See also* **riboflavin**.

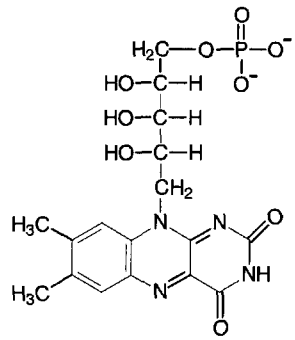


flavin-adenine dinucleotide (reduced) *abbr.*: $FADH_2$; adenosine diphosphate dihydroriboflavin; 1,5-dihydro-7,8-dimethyl-10-[5-(adenosine(5′)diphospho)-D- ribityl]isoalloxazine. The reduction occurs at the two unprotonated nitrogen atoms at positions 1 and 5 of FAD. *See* **flavin-adenine dinucleotide**.

flavin coenzyme a general name sometimes used for a **flavin nucleotide** when not covalently linked to an apoenzyme.

flavin enzyme *or* **flavoenzyme** any **flavoprotein** that is an enzyme.

flavin mononucleotide *abbr.*: FMN; riboflavin 5′-phosphate, 7,8-dimethyl-10-(5-phospho-D-ribityl)isoalloxazine. Although not strictly a mononucleotide, since it contains an alditol moiety rather than a glycose moiety, it nevertheless is considered as one (*see* **nucleotide** (def. 3)), and as such is a component of **flavin-adenine dinucleotide**. It forms the coenzyme (or occasionally the prosthetic group) of various flavoprotein oxidoreductase enzymes, where it functions as an electron acceptor by being reversibly converted to **flavin mononucleotide (reduced)**. *See also* **riboflavin**.



flavin mononucleotide (reduced) *abbr.* $FMNH_2$; dihydroriboflavin 5′-phosphate, 1,5-dihydro-7,8-dimethyl-10-(5-phospho-D-ribityl)isoalloxazine. The reduction occurs at the two unprotonated nitrogen atoms at positions 1 and 5 of FMN. *See* **flavin mononucleotide**.

flavin nucleotide a general name sometimes used for flavin-adenine dinucleotide and flavin mononucleotide, and their reduced forms.

flavin reductase *(in luminescent bacteria)* the product of the *luxG* gene in several marine luminescent bacteria. It is presumed from sequence similarity to be an FAD/NAD(P) flavoprotein oxidoreductase. Example from *Vibrio fischeri*: database code LUXG_VIBFI, 236 amino acids (26.47 kDa).

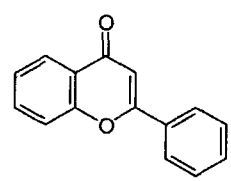
flavo+ *comb. form* **1** yellow. **2** containing a **flavin nucleotide**.

flavocytochrome any protein that is both a **flavoprotein** and a **cytochrome**, e.g. yeast L-lactate dehydrogenase (cytochrome), (EC 1.1.2.3), also known as **cytochrome b_2**.

flavodoxin any of a group of small protein electron carriers, widely distributed in anaerobic bacteria, photosynthetic bacteria, and cyanobacteria, that contain covalently linked flavin mononucleotide. They readily form stable blue semiquinones, and can substitute functionally for **ferredoxin**. Example from *Escherichia coli*: database code FLAV_ECOLI, 175 amino acids (19.58 kDa).

flavolans *see* **tannin**.

flavone **1** 2-phenylchromen-4-one; 2-phenyl-4*H*-1-benzopyran-4-one; a potent inhibitor of **prostaglandin-endoperoxide synthase**. **2** any of a group of hydroxylated derivatives of flavone. Flavone glycosides occur as pigments, usually yellow, in flowering plants and form one of the classes of **flavonoid** (def. 1). *Distinguish from* **flavanone**.



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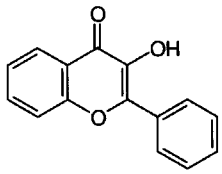
flavonoid **1** any of a very large and widespread group of water-soluble phenolic derivatives, often brightly coloured and usually found in the vacuoles of plant cells. They are glycosides with the structures of their aglycon moieties based on the **flavan** skeleton, and are classified according to the oxidation state of its pyran ring. Some 10–12 classes are recognized. **2** any flavone, isoflavone, or neoflavone, or any of their derivatives, including bioflavonoids. *See also* **apigenin**, **myricetin**, **quercetin**. **3** of, relating to, or resembling flavone, isoflavone, or neoflavone.

flavonol **1** 3-hydroxyflavone. **2** any of a group of hydroxylated derivatives of flavonol. Flavonol glycosides occur as pigments, usually yellow, in flowering plants, and form one of the classes of **flavonoid** (def. 1). *Distinguish from* **flavanol**.



flavoprotein *abbr.*: FP; any enzyme or other protein of which a flavin nucleotide is a coenzyme or prosthetic group. They occur in virtually all cells, where they act as oxidoreductases or as electron carriers in the terminal electron transport chains.

Fleming, (Sir) Alexander (1881–1955), British bacteriologist famous for his discovery of the bacteriolytic agents lysozyme and penicillin; Nobel Laureate in Physiology or Medicine (1945) jointly with E. B. Chain and H. W. Florey 'for the discovery of penicillin and its curative effect in various infectious diseases'.

Fletcher factor *see* **plasma kallikrein**.

flg *see* **fibroblast growth factor receptor**.

flickering cluster model a model for the structure of liquid water in which small, tetrahedrally coordinated, icelike regions, held together by hydrogen bonds, are thought to exist for short periods, continually breaking up and re-forming.

flightin the enzyme **glycerol 3-phosphate dehydrogenase (NAD+)** obtained from certain insects. It is so called because this and mitochondrial **glycerol 3-phosphate oxidase** play a major role in the transfer of energy needed for flight in insects.

flip-flop **1** *(in electronics)* a circuit or device having two stable states and two inputs corresponding to these states. The device remains in either state until caused to change to the other state by application of an appropriate signal to the inputs. **2** *(in enzymology)* a mechanism in which a functional interrelationship between distinct active sites on identical monomers, which are parts of an oligomeric enzyme showing Michaelian kinetics, is mediated by a structural modification, the **flip-flop transition**. *Compare* **half-of-the-sites reactivity**. **3** *(in genetics) the informal name for* a reversible, reciprocal exchange betweeen recombining segments of DNA in site-specific recombination systems in prokaryotes or eukaryotes. *See also* **transposable element**.

flipping *a jargon term used in* **nuclear magnetic resonance spectroscopy** *for* the change in orientation of an atomic nucleus from an angle $\theta°$ to $(180 - \theta)°$, with respect to the direction of the magnetic field, caused by absorption of radiation energy of a specific radiofrequency.

flocculate to aggregate or cause to aggregate into 'woolly' clusters or masses.

flocculation **1** the act or process of flocculating (*see* **flocculate**). **2** the product of such an act or process.

flocculation reaction *or* **flocculation test** a **precipitin test** in which the precipitate appears as floccules.

floccule a small aggregated mass of flocculent material.

flocculent **1** having the appearance of wool or down. **2** *(in chemistry)* consisting of or occurring as small woolly or downy aggregates. **3** *(in biology)* covered with waxy flakes or tufts resembling wool.

flora **1** *collective term for* all the plants, or plant life, characteristic of a given place or period. **2** microbial flora; the microbial population of part of the body, e.g. of the gut, skin, etc. **3** a comprehensive treatise or list of all the plants or plant life of a particular region or period.

Florey, (Sir) Howard Walter, Lord Florey (1898–1968), Australian physiologist and experimental pathologist distinguished particularly for his role in the development of penicillin (with E. B. Chain) and cephalosporin C as clinically useful antibacterial agents; Nobel Laureate in Physiology or Medicine (1945) jointly with E. B. Chain and A. Fleming 'for the discovery of penicillin and its curative effect in various infectious diseases'.

Florisil *the proprietary name for* a type of activated magnesium silicate. It is an adsorbent and is useful for column chromatographic separation of lipids.

flotation coefficient a name sometimes given to a negative **sedimentation coefficient**.

flow birefringence *or* **double refraction of flow** the **birefringence** induced in a fluid by shear, which causes orientation of any asymmetric molecules in the fluid.

flow cabinet another name for **safety cabinet**.

flow cell any **cell** (def. 2) so constructed that appropriate measurements (as of absorbance) may be made on a flowing fluid.

flow cytofluorimeter a **flow cytometer** in which fluorescence of the objects being counted is monitored.

flow cytometer an apparatus for **flow cytometry** in which cells, or subcellular components (e.g. isolated chromosomes), in aqueous suspension are made to flow at high speed, in single file, through a sensing region where optical or electric signals indicative of some important physical or chemical properties of the cells, or components, are generated. These signals are analysed and accumulated in a computer for quantitative evaluation. Typical flow rates that can be achieved are in the region of 1000 cells per second. *See also* **flow sorter**, **fluorescence-activated cell sorter**.

flow cytometry the technique for counting or measuring some property of cells, or subcellular components, using a **flow cytometer**, often after labelling with a fluorescent marker.

flow dichroism **dichroism** (def. 1) induced in a fluid by shear, which causes orientation of any asymmetric molecules in the fluid.

flower the reproductive structure of angiosperm plants. It consists generally of sepals, petals, and stamens and/or carpels. It is basically a highly modified leafy shoot.

flow-signal *an earlier term for* **rheoseme**.

flow sorter (for cells) a **flow cytometer** to which has been added a device for physically separating cells, or subcellular components, of desired characteristics in order to provide subpopulations of high homogeneity. Typically the cell suspension is forced out of an orifice, 50–100 μm in diameter, forming a high-speed liquid jet in air. Optical sensing of the jet takes place near the orifice and the jet is then broken up into uniform droplets by applied ultrasonic vibration. The droplets then traverse a region of high-intensity constant electric field where the decision-making and charging circuits, activated by the sensors, cause only droplets containing the wanted cells to be charged and deflected by the electric field into a separate collector.

fluctuation test a method of statistical analysis used to determine whether selected variants, e.g. phage- or drug-resistant bacterial mutants, arose spontaneously prior to exposure to the selective agent or were caused by the agent.

fludrocortisone 9α-fluorohydrocortisone (11β)-9-fluoro-11,17,21-trihydroxypregn-4-ene-3,20-dione; a **corticosteroid** with about 10 times the glucocorticoid action of cortisol, but with 300–600 times greater mineralocorticoid action. It is used topically in ointments.

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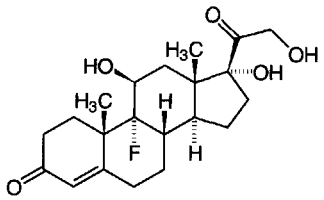


fludrocortisone

fluence *symbol*: *F* or *H*; *(in photochemistry)* the energy delivered in a given time interval, d*t*; $F = \int I dt$ where *I* is the radiant intensity and *t* is time. It is expressed in J m^{-2}.

fluence rate **fluence** per unit time; it is commonly referred to (strictly incorrectly) as **flux**.

fluid **1** any substance that can flow; any portion of matter in which the components (molecules or particles) continuously change their relative positions. In physics, the term comprehends any liquid or gas; in biology (and in common usage) it generally denotes only a liquid, especially one present in, or secreted by, a living organism. **2** able to flow or to change shape easily; not solid or rigid; liquid. **3** of, concerned with, or using fluid, a fluid, or fluids.

fluidity *(in physics)* the reciprocal of the **viscosity** of a fluid.

fluid mosaic model a model of cell-membrane structure in which the proteins that are integral to the membrane are considered as a heterologous set of globular molecules, each arranged in an amphipathic structure, i.e. with their ionic and highly polar groups protruding from the membrane into the aqueous phase and their nonpolar groups largely buried in the hydrophobic interior of the membrane. These globular molecules are partially embedded in a matrix of phospholipid, the bulk of which is organized as a discontinuous, fluid bilayer, although a small fraction of the lipid may interact specifically with the membrane proteins. Thus the fluid mosaic structure is formally analogous to a two-dimensional oriented solution of integral proteins (or lipoproteins) in a viscous phospholipid bilayer solvent.

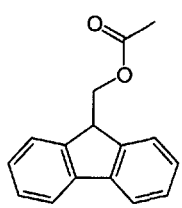
Fluon *a proprietary name for* **polytetrafluorethylene**.

fluor *or* **lumiphor** *or* **scintillator** any substance that displays **fluorescence** when excited by electromagnetic or particulate radiation. Fluors are useful especially in **scintillation counters**.

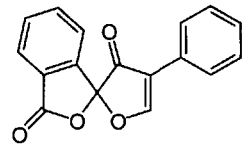
fluor+ *a variant form of* **fluoro+** (sometimes before a vowel).

fluoracetate *see* **fluoroacetate**.

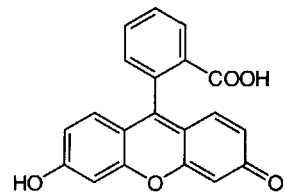
fluorenylmethoxycarbonyl *symbol*: Fmoc; *abbr.*: FMOC; fluoren-9-ylmethoxycarbonyl; a group used for linkage to amino groups for the purpose either of forming fluorescent amino-acid derivatives that can readily be detected after column chromatography, or to protect the amino groups of amino acids or nucleotides while other functional groups are undergoing reaction. Reagents useful for introducing the group are 9-fluorenylmethyl chloroformate and 9-fluorenylmethyl succinimidyl carbonate.



fluorescamine 4-phenylspiro[furan-2(3*H*),1′-(3′*H*)-isobenzofuran]-3,3′-dione; a nonfluorescent compound forming fluorescent structures on reaction with primary amines. *Proprietary name*: Fluram.



fluorescein 9-(2-carboxyphenyl)-6-hydroxy-3*H*-xanthen-3-one; Acid Yellow 73; CI 45350; an orange-red dye, the sodium salt of which is freely soluble in water to give a solution with yellowish-green fluorescence (to a dilution of 0.02 ppm) under UV light. Certain derivatives, e.g. fluorescein isothiocyanate, are useful for **fluorescein labelling** and others, e.g. the nonfluorescent fluorescein diacetate, are useful as substrates for the detection and assay of esterases.



fluorescein labelling the introduction of fluoresceinyl groups (*see* **fluorescein**) into biopolymers for fluorescence polarization studies and fluorescence immunoassay techniques.

fluorescence **1** a type of luminescence that consists of the emission by a substance of electromagnetic radiation, especially visible light, as a result of and immediately (10–100 ns) after the absorption of energy derived from exciting radiation of another, usually shorter, wavelength or from incident subatomic particles (especially electrons or alpha particles); the property of emitting such radiation. **2** the radiation emitted during **fluorescence** (def. 1). *Compare* **phosphorescence**. —**fluorescent**, **fluorescing** *adj.*; **fluoresce** *vb.*

fluorescence-activated cell sorter *or* **fluorescence-assisted cell sorter** *abbr.*: FACS; a type of **flow sorter** in which cells are characterized and sorted by the intensity of the fluorescence they emit when passing through an exciting laser beam.

fluorescence depolarization *or* **depolarization of fluorescence** the phenomenon occurring when fluorescence is excited by plane polarized radiation; the emitted radiation is always partially depolarized (*see* **fluorescence polarization**). The extent of such depolarization is due, *inter alia*, to the motion of the absorber (i.e. Brownian motion) and to energy transfer between like chromophores. Fluorescence depolarization can be used to follow the changes in the motion (rotation) of an entire macromolecule, or of a part of the molecule, to which fluorescent chromophores are attached; it can also be used to indicate the environment of a **fluorescent probe** in, e.g., a membrane – an environment that results from less tightly packed structures permits greater movement of the probe molecule, thus leading to greater depolarization. *See also* **photon counter**, **time-resolved fluorescence polarization**.

fluorescence energy transfer a process of energy transfer between two **fluorophors**, which can occur when the emission spectrum of the first fluorophor overlaps the absorption spectrum of the second fluorophor. **Quenching** of the emission from the first compound occurs but the excitation energy is absorbed by the second compound, which then emits its own characteristic fluorescence. If the two fluorophors are attached at different positions to a macromolecule, observations

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of fluorescence energy transfer between them may be used to determine the distance between the two attachment positions.

fluorescence enhancement *or* **enhancement of fluorescence** a phenomenon occurring with a number of **fluorophors** whose fluoresence is markedly dependent on the polarity of the medium, in which fluorescence is greatly enhanced in a nonpolar or rigid environment, but strongly quenched in an aqueous environment. Examples are 8-anilinonaphthalene sulfonate (**ANS**) when bound to an antibody or trapped in the hydrophobic environment within a protein; and ethidium when intercalated into double-helical regions of a nucleic acid.

fluorescence immunoassay *or* **fluorescent immunoassay** *or* **fluoroimmunoassay** *abbr.*: FIA; a method of assaying very small amounts of material that is similar in principle to **radioimmunoassay** but uses a fluorescent rather than a radioactive label for the antigen. Various techniques can be used for determination of the ratio of bound to free labelled antigen that do not necessitate a separation of the two; these may depend instead on **fluoresence energy transfer**, **fluorescence enhancement**, **fluorescence depolarization**, **fluorescence quenching**, or other phenomena.

fluorescence *in situ* hybridization *abbr.*: FISH; a procedure that involves the use of DNA probes to locate in a tissue section specific regions of DNA in the chromosomes. The probes are tagged with a selection of fluorescent molecules that are both excited by and emit light of different wavelengths and hence different colours. The structure and behaviour of individual chromosomes at all stages of the cell cycle can thereby be studied.

fluorescence microscopy a type of light microscopy by means of which fluorescent substances in a specimen may be detected and examined. Exciting light, commonly UV and of appropriate wavelengths, is isolated by means of a suitable filter placed between the light source and the condenser, and emitted radiation is selected by a different filter placed between the objective lens and the eye-piece. The technique is useful for visualizing certain components that are difficult to see by direct light, for localizing fluorescent substances bound to specific components of the specimen, and for determining the orientation of a specimen using the **fluorescence depolarization** technique.

fluorescence photobleaching recovery *an alternative name for* **fluorescence redistribution after photobleaching**.

fluorescence polarization *or* **polarization of fluorescence** the phenomenon that the light emitted from a fluorescent molecules is always partially polarized. This is true whether or not the exciting radiation is plane polarized. In consequence, when plane polarized radiation is used to excite fluorescence, **fluorescence depolarization** occurs.

fluoresence probe *or* **fluorescent probe** any small molecule that undergoes changes in one or more of its fluorescence properties as a result of noncovalent interaction with a protein or other macromolecular structure. Such probes are useful for studying the properties and behaviour of macromolecules. *See* **probe** (def. 1).

fluorescence quantum yield in any fluorescent system, the ratio of the number of photons emitted to the number of photons absorbed; the fraction of excited singlets that become de-excited by fluorescence. *See also* **quantum yield** (def. 1).

fluorescence quenching the reduction in the **fluorescence quantum yield** of a system due to de-excitation of the fluorescent molecules by environmental factors such as collision or complex formation with quenchers in the system, or by **fluorescence energy transfer** to them. The phenomenon is useful in studies of the binding of small molecules to proteins and other macromolecules.

fluorescence redistribution after photobleaching *abbr.*: FRAP; a technique, also termed **fluorescence photobleaching recovery**, for measuring two-dimensional lateral mobility of fluorescent particles in small (≈10 μm^2) regions of a cell surface. A small spot on the surface is photobleached by a brief exposure to an intense, focused laser beam, and the subsequent recovery of fluorescence, due to replenishment of intact fluorophor in the bleached spot by lateral transport from the surrounding surface, is followed.

fluorescence spectrophotometry the measurement, by means of a **spectrofluorometer**, of the wavelengths and the intensities of the light emitted from a fluorescent sample that is excited by more or less monochromatic exciting radiation.

fluorescence spectrum the **emission spectrum** of a fluorescent system that is excited by radiation of a given wavelength. *Compare* **excitation spectrum**.

fluorescent antibody technique an **immunofluorescence** technique in which antibody conjugated with a fluorophor is used to locate corresponding antigen in tissue sections or smears.

fluorescent immunoassay *a variant spelling of* **fluorescence immunoassay**.

fluorescent probe *a variant spelling of* **fluorescence probe**.

fluorescent screen a screen coated with a substance, e.g. zinc sulfide or calcium tungstate, that fluoresces when irradiated with electromagnetic radiation of certain wavelengths or with particulate radiation.

fluori+ *a variant form of (sometimes before a vowel)* **fluoro+**.

fluoridation the addition of up to approximately 1 ppm of fluoride ion to a drinking water supply with the object of reducing tooth decay in consumers of the water. —**fluoridate** *vb.*

fluorimeter *a variant spelling of* **fluorometer**.

fluorinate **1** to treat or react (a substance) with difluorine. **2** to introduce (one or more) fluorine atoms into (a molecule of an organic compound), whether by addition or by substitution. —**fluorinated** *adj.*; **fluorination** *n.*

fluoro+ *or (sometimes before a vowel)* **fluor+** *comb. form* **1** denoting a fluorine in organic linkage. **2** *or* **fluori+** indicating fluorescence.

fluoroacetate the anion of fluoroacetic acid (= fluoroethanoic acid); a toxic substance found in the leaves of *Dichapetalum cymosum* and other plants that in animals is converted enzymically into **fluorocitrate**. Fluoroacetate and fluoroacetamide have been used as rodenticides.

fluorochrome any substance exhibiting fluorescence, especially one used to impart fluorescence to another molecule or to a specific structure in a biological specimen.

fluorocitrate the trianion of 1-fluoro-2-hydroxy-1,2,3-propanetricarboxylic acid; an extremely toxic substance formed in animal tissues from fluoroacetate. Fluorocitrate is a potent inhibitor of aconitase; it is believed that the fluorine atom interacts strongly with the Fe^{2+} ion at the active centre of the enzyme thereby inhibiting its activity. *See also* **lethal synthesis**.

fluorodeoxyuridine *see* **fluorouracil**.

fluorodeoxyuridylate *see* **fluorouracil**.

fluorodinitrobenzene *see* **Sanger's reagent**.

fluorogen the nonfluorescent precursor of a **fluorophor**.

fluorogenic **1** producing fluorescence. **2** of or pertaining to a **fluorogen**; e.g. a *fluorogenic substrate* is a nonfluorescent material that can be acted on by an enzyme to produce a fluorescent substance.

fluorogram **1** *or (sometimes)* **autofluorogram** an autographic image derived by **fluorography** (def. 1). **2** *or* **fluorograph** a photographic image produced by **fluorography** (def. 2).

fluorography **1** *or* **autofluorography** *or* **scintillation autography** *or* **scintillation autoradiography** an elaboration of autoradiography that shows a considerable increase in the efficiency of detection of low-energy-beta-particle-emitting nuclides, e.g. carbon-14, sulfur-35, and (especially) tritium, in preparations such as thin-layer chromatograms, gel electrophoretograms, tissue or whole-body sections, etc. The otherwise poor response of autoradiography in these situations results from internal absorption of most of the emitted radiation by the specimen in question. In fluorography this effect is diminished by impregnating the specimen (which preferably should be translucent and colourless) with fluor(s) prior to placing it in

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contact with an appropriately sensitive photographic emulsion or film, which then responds both to direct emission of beta particles from the specimen and to emission of photons of UV light (scintillations) generated by beta particles, exciting the fluor within the specimen. **2** photography of a fluorescent body, especially of an image on a fluorescent screen. —**fluorograph** *n.*, *vb.*; **fluorographic** *adj.*

fluoroimmunoassay *abbr.*: FIA; *a variant spelling of* **fluorescence immunoassay**.

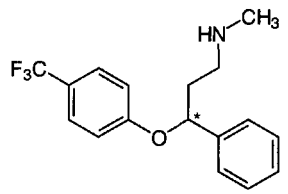
fluorometer *or* **fluorimeter** **1** a device for measuring the intensity and duration of fluorescence. **2** a device that may be attached to a **fluoroscope** to enable the position of a sought object to be determined with precision. —**fluorometric** *or* **fluorimetric** *adj.*; **fluorometry** *or* **fluorimetry** *n.*

fluorophor *or* **fluorophore** **1** a group of atoms in a molecule that renders the latter fluorescent. **2** a fluorescent substance.

fluoroscope **1** a screen coated with a substance that fluoresces when excited by X-rays; it is used to view the X-ray image of an object. **2** a device used to compare the fluorescence of a solution with that of a standard.

fluorouracil *symbol*: FUra (*not* FU); 5-fluorouracil; 5-fluoro-2,4(1*H*,3*H*)-pyrimidinedione; a synthetic analogue of uracil that is enzymically converted via its β-D-ribofuranoside, fluorouridine (*symbol*: FUrd), to fluorodeoxyuridine (*symbol*: FdUrd) and then to fluorodeoxyuridylate, which is a potent inhibitor of **thymidylate synthase** and, hence, of DNA synthesis. Thus fluorouracil is a **suicide inactivator** of thymidylate synthase. Fluorouracil and fluorodeoxyuridine are anticancer drugs, commonly used in combination therapy against fast-growing tumours.

fluoxetine (±)–*N*-methyl-γ-[4-(trifluoromethyl)phenoxy]benzenepropanamine; a serotonin uptake inhibitor, used as an antidepressant, particularly as the hydrochloride (*proprietary name*: Prozac).



* = racemic

flush end *or* **blunt end** an end of a duplex DNA fragment in which the two strands are coextensive, i. e. terminate at the same point. Such ends may be formed by scission of duplex DNA with some types of endonucleases. *Compare* **cohesive end**. —**flush-ended** *adj.*

flux **1** the rate of passage of energy or matter (usually in crossing a given area or passing through a given volume) under steady-state conditions. *See* **diffusion coefficient**, **luminous flux**, **radiant power**. **2** the number of particles passing through unit cross-sectional area of beam per unit time. **3** the rate of (chemical or physical) transformation of a substance within a living cell or tissue; the rate of translocation of a substance within a living cell or tissue, especially across a cell membrane. Such processes are usually measured in moles per second. *See also* **metabolic flux**. **4** the strength of a field of force orthogonal to unit area. *See* **magnetic flux**. **5** *an alternative term for* **flux density** (def. 2).

flux control coefficient *symbol*: C_E^J; in a metabolic sequence at steady state, the response, δ*J*, of the original system flux, *J*, to a small change, δE, in either the concentration or one of the kinetic parameters of a specified enzyme, E; it is given by:

$$C_E^J = (\frac{\partial J/J}{\partial E/E})\, p, q, r, \ldots$$

and similarly for every other enzyme in the system. This is the flux control coefficient of the enzyme E on the flux *J*, and is also called **sensitivity coefficient** or **control strength**. Similarly one can calculate a flux control coefficient for the substrate concentration, *S*, on the flux, *J* (this is also called **sensitivity** or **net sensitivity**) and a flux control coefficient of an effector concentration, *I*, on the flux, *J* (this is also called **control strength**).

flux density **1** (of energy or field strength) the **flux** per unit cross-sectional area; *see* **luminous flux density**, **magnetic flux density**. **2** *or (sometimes)* **flux** (of particulate radiation, including photons) the arithmetic product of the particle density and the mean velocity of the particles; **neutron flux (density)**.

flux-ratio method a method for investigating the mechanisms of enzymic reactions in which simultaneous measurements are made of the rates of enzyme-catalysed isotopic transfers from one product to two substrates while the reaction system is in a steady state. It provides relatively unambiguous information about the order of binding of substrates.

Fm *symbol for* fermium.

fMet *symbol for* a residue of the α-acylamino acid *N*-formyl-L-methionine.

FMN *abbr. for* flavin mononucleotide.

FMN adenylyltransferase EC 2.7.7.2; *other name*: FAD pyrophosphorylase; an enzyme of the pathway for biosynthesis of FAD. It catalyses the reaction of ATP with FMN to form FAD with release of pyrophosphate.

$FMNH_2$ *symbol for* flavin mononucleotide (reduced).

Fmoc *symbol for* the fluorenylmethyloxycarbonyl group.

FMOC *abbr. for* the fluorenylmethyloxycarbonyl group.

fmol *symbol for* femtomole (10^{-15} mole).

FMS *symbol for* either the retroviral **oncogene**, v-*fms*, which is carried by the McDonough strain of feline sarcoma virus, or its related protooncogene, c-*fms*, which encodes the M-CSF-1 receptor precursor (*see* **colony stimulating factor**). The latter is a type I transmembrane protein of the immunoglobulin superfamily; database code KFMS_HUMAN, 972 amino acids (107.83 kDa). It possesses intrinsic protein tyrosine kinase activity within its cytoplasmic domain, which is activated by the binding of CSF-1 (*see* **colony stimulating factor**) to the extracellular domain. Its transforming counterpart, v-*fms*, encodes a constitutively active receptor kinase that can transform both fibroblasts and hematopoietic cells in a CSF-1-independent manner. Mutations in the c-*fms* gene as well as a critical alteration of the 3′ coding sequences appear to be responsible for fully activating its latent transforming potential. In the v-*fms* protein product, 40 C-terminal amino acids of the normal CSF-1 receptor are replaced by 11 unrelated residues, suggesting that residues near the C terminus normally negatively regulate kinase activity in the absence of CSF-1.

f-number the numerical value of the relative aperture of a lens; it is the ratio of the focal length of a lens to its diameter.

foam **1** a dispersion in which a large proportion of gas by volume, in the form of gas bubbles usually >1 μm in diameter, is dispersed in a liquid, solid, or gel. **2** to produce or cause to produce such a foam.

foam fractionation a method of separation in which a component of the bulk liquid is preferentially adsorbed at the liquid/vapour interface and is removed by foaming.

foaming agent a **surfactant** that when present in small amounts facilitates the formation of a foam and/or stabilizes it.

focal contact any of the areas on the surface of fibroblasts where actin-containing microfilaments terminate. The filaments are involved both in the attachment of the cells to the substrate and in cell movement.

fodrin *or* **brain spectrin** *or* **calspectin** a protein from bovine brain, immunologically related to **spectrin**, that is involved in secretion, interacts with calmodulin in a calcium-dependent manner, and thus is a candidate for the calcium-dependent movement of the cytoskeleton at the membrane. It contains 20 repeats of 106 amino-acid residues; example from mouse (partial sequence): database code FODA_MOUSE, 381 amino

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acids (43.26 kDa).

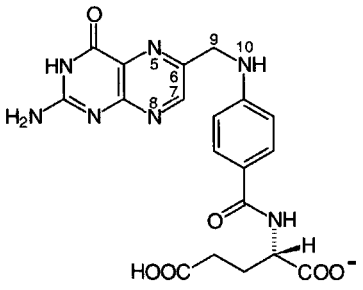
foetal *a variant spelling of* fetal (*see* **fetus**).

foeto+ *a variant spelling of* **feto+**.

foetus *an etymologically misconceived variant spelling of* **fetus**.

folacin *a common name for* **folic acid**.

folate **1** *the recommended trivial name for* pteroylglutamate; *N*-[4-{[(2-amino-3,4-dihydro-4-oxopteridin-6-yl)methyl]-amino}benzoyl]-L-glutamate; the anion of **folic acid** (def. 1). **2** any member of the family of pteroylglutamates, irrespective of the level of reduction of the pteridine ring, of the nature of any one-carbon substituent, and of the number of glutamate residues. *See also* **folic acid** (def. 2).



folate coenzyme any of various interconvertible tetrahydrofolates that bear a one-carbon substituent and function as coenzymes in metabolic reactions involving the transfer of one-carbon units. The substituent may be 5-formimino, 5-formyl, 10-formyl, 5,10-methenyl, 5-methyl, or 5,10-methylene.

Folch–Lees protein the most abundant type of protein that is extractable from central-nervous-system myelin by chloroform:methanol (2:1 v/v); it is of at least 150 kDa and contains a high proportion of aliphatic amino acids. *Compare* **Wolfgram proteolipid protein**.

Folch method a method for the fractionation and isolation of lipids from either tissues or fluids. It involves extraction with various chloroform–methanol–water mixtures.

fold a description of protein conformations; there is no universally agreed criterion for proteins to be regarded as having the same fold but folds appear in the SCOP and CATH hierarchies (*see* Appendix E, Table 3).

foldback DNA *an alternative term for* hairpin DNA. *See* **hairpin**.

folding *(in molecular biology)* **1** the process whereby an unorganized polypeptide acquires a specific three-dimensional structure. **2** the detailed pattern of three-dimensional structure of a native protein molecule.

folding unit a locally ordered region within the hydrophobic core of a globular protein molecule, formed by three-dimensional interaction between two or three segments of secondary structure (α helix and/or β strand) that are near one another along the polypeptide chain. The most important types are: (αα), (αβ), (βββ), (βαβ). *See also* **domain**.

folic acid *abbr.*: (not recommended) FA *or* F; **1** *the recommended trivial name for* pteroylglutamic acid, the corresponding acid of **folate** (def. 1). **2** *or* **folacin** the name under which any **folate** (def. 2) is generally known in medicine, nutrition, etc. Folic acids are widely distributed members of the vitamin B complex, particularly plentiful in green leafy vegetables, liver, and yeast. Folates are essential for the synthesis of purines and pyrimidines, functioning as carriers of one-carbon units. A deficiency in humans results in megaloblastic anemia and in birth defects in children born to deficient mothers. Folic acids are also growth factors for certain microorganisms. *See also* **folinic acid**.

folic acid conjugate the corresponding acid of any **folate** (def. 2) containing two or more glutamyl residues.

folic acid reductase *an alternative name for* **dihydrofolate reductase**.

Folin–Ciocalteau reagent a phosphomolybdotungstic acid reagent that gives a blue colour with phenols. The reagent has been used in the determination of tryptophan and tyrosine in proteins and peptides. *See also* **Lowry method**.

folinic acid **1** *or (formerly)* **citrovorum factor** (*abbr.*: CF) *or (formerly)* **leucovorin** *or* **5-formyltetrahydrofolic acid** 5-formyl-5,6,7,8-tetrahydropteroyl-L-glutamic acid; the common name for the corresponding acid of **folinate** (5-formyltetrahydrofolate), a folate coenzyme discovered to be a growth factor for the bacterium *Leuconostoc citrovorum* (hence its former synonyms). Folinate is an intermediate in the metabolic conversion of formiminoglutamate to glutamate, ammonium, and **active one-carbon**. The calcium salt, calcium folinate (*or formerly* calcium leucovorin), is useful therapeutically, e.g. as an antidote to doses of methotrexate or other folate antagonists. **2** *name sometimes used for* certain other folates, e.g. tetrahydrofolate, especially as growth factors for microorganisms.

Folin–Lowry method a sensitive method of protein assay in which protein reacts both with an alkaline copper tartrate solution and with the **Folin–Ciocalteu reagent** to give a blue colour, the absorbance of which is measured at 750 nm. *Compare* **Lowry method**.

Folin reaction a colorimetric reaction used for the determination of ammonia and amino-acid nitrogen in which a red colour is produced when an alkaline solution of amino acids is treated with 1,2-naphthoquinone-4-sulfonate. [After Otto Knute Olof Folin (1867–1934).]

Folin–Wu reagent a phosphomolybdic acid solution, containing a little tungstate, used in the determination of glucose. It gives a blue colour with the copper (I) oxide produced when the sample containing glucose is heated with an alkaline copper (II) solution. [After Otto Knute Olof Folin (1867–1934) and Hsien Wu (1893–1959).]

folliberin *the recommended name for* follicle-stimulating hormone releasing hormone (*abbr.*: FSH-RH or FRH). Luteinizing hormone releasing hormone (*abbr.*: LHRH) stimulates not only release of luteinizing hormone from the anterior pituitary but also release of follicle-stimulating hormone. This activity is commonly named **gonadotropin-releasing hormone**. There is, however, evidence that a specific FSH-RH may exist in addition.

follicle **1** any small cavity or recess. **2** a cavity that has a secretory or excretory function, e.g. the **Graafian follicle**.

follicle-stimulating hormone *abbr.*: FSH; *recommended name*: follitropin; one of two gonadotropic **glycoprotein hormones** secreted by the anterior pituitary; of 34 kDa (human), 33 kDa (ovine), or 29 kDa (porcine), it consists of α and β subunits, the α subunit being almost identical within a given species to that of other glycoprotein hormones and the β subunit conferring hormonal specificity; the carbohydrate content is 16% (human), 8–9% (ovine), or 7–8% (porcine). In the female it stimulates the growth of Graafian follicles in the ovaries, whereas in the male it stimulates the epithelium of the seminiferous tubules to increased spermatogenesis. Example, β subunit from *Bos taurus*: database code FSHB_BOVIN, 129 amino acids (14.71 kDa).

follicle-stimulating hormone releasing factor (*abbr.*: FRF *or* FSH-RF) *or* **follicle-stimulating hormone releasing hormone** (*abbr.*: FRH *or* FSH-RH) *see* **gonadotropin-releasing hormone**.

follicular **1** like, pertaining to, consisting of, or provided with a follicle or follicles. **2** affecting or involving follicles.

follicular phase *see* **estrous cycle**.

folliculate(d) having or consisting of follicles.

follipsin a serine proteinase from pig ovarian fluid. It is a heterodimer, and cleaves Arg-|-Xaa bonds.

follistatin an **activin**-binding glycoprotein that regulates biosynthesis and secretion of **follicle-stimulating hormone**. Alternative isoforms are formed by alternative splicing. Example

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(precursor) from human: database code FSA_HUMAN, 338 amino acids (37.33 kDa).

follitropin *the recommended name for* **follicle-stimulating hormone**.

folyl *the trivial name for* pteroylglutamyl, the acyl group derived from **folic acid** (def. 1). Use of the name is no longer recommended.

fomecin any of several antibiotic substances produced by certain strains of the basidiomycetous fungus *Fomes juniperinus*, especially fomecin A, 2,3,4,-trihydroxy-6-(hydroxymethyl) benzaldehyde.

food any material that can be ingested by an organism and metabolized to provide energy and precursors for biosynthetic reactions.

footprinting a technique for identifying sites where there is protein bound to DNA. Protein–DNA complexes are resistant to the action of nucleases, so that undegraded DNA (the 'footprint') remains after treatment with a nuclease.

For *symbol for* the formyl group, H–CO– (alternative to HCO).

Forbes' disease *an alternative name for* type III **glycogen disease**. [After Gilbert Burnett Forbes (1915–), US physician.]

forbidden clone a hypothetical clone of immunologically competent cells with specificity for some autoantigen that, in accord with the clonal selection theory, has become suppressed in the fetus but may be reactivated in adult life and cause an autoimmune disease.

forbidden transition any transition between energy states in an atom or molecule that is forbidden by the selection rules of quantum mechanics (but can occur nevertheless!).

force *symbol*: *F (in physics)* a vector quantity, the external influence that changes or tends to change the state of rest or uniform motion of a body, or the shape of a fixed body. The SI derived unit of force is the **newton**.

formaldehyde dismutase EC 1.2.99.4; *systematic name*: formaldehyde:formaldehyde oxidoreductase. An enzyme that catalyses a dismutation of two molecules of formaldehyde to formate and methanol. The enzyme functions to detoxify formaldehyde thus rendering the organism resistant to formaldehyde. Its synthesis is induced by addition of formaldehyde to the medium. Example from *Pseudomonas putida* (strain F61) DNA: database code PSEFDM, 399 amino acids (42.93 kDa).

formaldehyde transketolase EC 2.2.1.3; *systematic name*: D-xylulose-5-phosphate:formaldehyde glycolaldehydetransferase; *other names*: dihydroxyacetone synthase; DHAS; glycerone synthase. An enzyme that catalyses a reaction between D-xylulose 5-phosphate and formaldehyde to form glyceraldehyde 3-phosphate and glycerone; thiamine diphosphate is a coenzyme. The enzyme is important in organisms (some fungi and many prokaryotes) that can utilize methanol as a carbon source in converting formaldehyde, produced by methanol oxidation, into carbohydrate, xylulose 5-phosphate acting as C_2 donor. Example from *Hansenula polymorpha* (a species of yeast): database code DAS_HANPO, 710 amino acids (78.75 kDa).

formalin *or* **formol** a 40% w/v aqueous solution of formaldehyde stabilized with approximately 12% v/v methanol. It is useful as a general disinfectant and for fixation and preservation of biological specimens.

formate **1** *trivial and preferred name for* **methanoate**, the anion, $H–COO^-$, derived from formic acid (methanoic acid). **2** any mixture of formic acid and its anion. It is useful as a buffer over the pH range 2.6–4.8; pK_a (25 °C) = 3.75. **3** any salt or ester of formic acid.

formate–dihydrofolate ligase EC 6.3.4.17; *systematic name*: formate dihydrofolate ligase (ADP-forming); an enzyme that catalyses the formation of 10-formyldihydrofolate from ATP, formate, and dihydrofolate with release of ADP and orthophosphate.

formate–tetrahydrofolate ligase EC 6.3.4.3; *systematic name*: formate:tetrahydrofolate ligase (ADP forming); *other name*: formyltetrahydrofolate synthetase; an enzyme involved in one of the transformations between **folate coenzymes**. It catalyses the formation of 10-formyltetrahydrofolate from ATP, formate, and tetrahydrofolate with release of ADP and orthophosphate. It is one of three enzymes (*see also* **methylenetetrahydrofolate dehydrogenase (NADP+)** and **methenyltetrahydrofolate cyclohydrolase**) necessary for the biosynthesis of purines, thymidylate, methionine, histidine, pantothenate, and formyl tRNA-Met. It is one activity of the trifunctional enzyme **C1-tetrahydrofolate synthase**. *See* **methylenetetrahydrofolate dehydrogenase (NADP+)** for an example.

formation constant *an alternative name for* **stability constant**.

formation function *see* **Bjerrum formation function**.

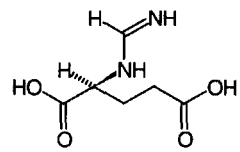
formazan **1** the compound $NH_2–N=CH–N=NH$. **2** any substitution derivative of this compound. Many are brightly coloured and may be reversibly oxidized into the corresponding colourless tetrazolium compounds (*see also* **Blue Tetrazolium**). Formazans prepared by coupling the phenylhydrazones of acyclic aldoses with diazonium compounds are useful in characterizing such sugars.

formed elements of the blood a general term for the **erythrocytes**, **leukocytes**, and **platelets**.

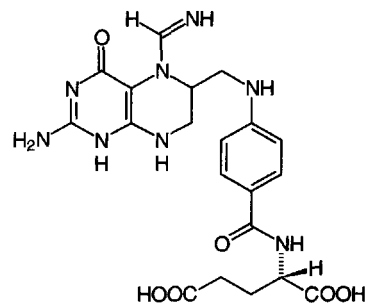
formimidoyl the acyl group, CH(=NH)–, derived from (the hypothetical) formimidic acid; the latter may also be regarded as the imino tautomer, CH(=NH)–OH, of formamide; hence also known as **formimino**.

formimino *see* **formimidoyl**.

formiminoglutamate *abbr.*: FIGLU; *N*-formimidoyl-L-glutamate; formamidino-L-glutarate; an intermediate in the catabolism of histidine. Its formimino (= formimidoyl) group is transferred to tetrahydrofolate to produce **5-formiminotetrahydrofolate**. In folate (or vitamin B_{12}) deficiency FIGLU accumulates in the tissues and its excretion in the urine increases. Estimation of the level of FIGLU in the urine is useful in assessing the extent of folate (or vitamin B_{12}) deficiency.



5-formiminotetrahydrofolate a derivative of tetrahydrofolate that is an intermediate in the metabolism of one-carbon units. It is formed from tetrahydrofolate and **formiminoglutamate**, and with **cyclodeaminase** yields 5,10-methenyltetrahydrofolate.



formin one of several developmental nuclear phosphoproteins found in several tissue types. They are formed by alternative splicing of the mouse *ld* (limb deformity) gene. Mutations in this locus result in defects of growth and patterning of the limb, and kidney during embryonic development. Example

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from *Mus musculus*: database code FORM_MOUSE, 1468 amino acids (163.62 kDa).

formol *(formerly) a proprietary name for* **formalin**.

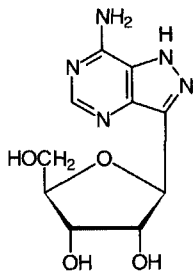
formolize *or* **formolise** to react the amino groups of amino acids, peptides, or proteins with formaldehyde.

formol titration the pH titration, with alkali, of amino acids, peptides, or proteins in the presence of formaldehyde. The formaldehyde reacts with the amino groups and lowers their apparent p*K* values, allowing identification of the region in the titration curve where they are being titrated.

formula (*pl.* **formulas** *or* **formulae**) **1** *(in chemistry)* a collection of symbols of atoms and numbers giving information about the composition and structure of a molecular chemical entity. **2** *(in mathematics)* a general relationship, principle, or rule expressed in symbols, frequently as an equation. **3** a recipe, or prescription, for the preparation of a medicine, food, etc. giving the constituents, their amounts, and the method to be used.

formula weight *a former name for* **relative formula mass**.

formycin either of two related **nucleoside antibiotics** synthesized by the actinomycete *Nocardia interforma* that display antitumour activity. **Formycin A**; 8-aza-9-deazaadenosine; 7-amino-3-(β-D-ribofuranosyl)-1*H*-pyrazolo[4,3-*d*]pyrimidine; an analogue of adenosine that inhibits *de novo* purine biosynthesis in tumour cells and is incorporated into RNA. It is deaminated in erythrocytes to **formycin B**, a competitive inhibitor of NAD^+ in the action of NAD^+ ADP-ribosyltransferase and an inhibitor of purine nucleoside phosphorylase.



formycin A

formyl *symbol*: For *or* HCO; the acyl group, H–CO–, derived from formic acid.

formylate to introduce (one or more) formyl groups into an organic compound. —**formylation** *n*.

***N*-formylmethionine** *symbol*: fMet; *codon*: AUG (when used as start codon for initiation) or GUG (when present as the first codon; within genes GUG encodes valine); a modified amino-acid residue which is found at the N terminus of nascent polypeptide chains in prokaryotes and bacteriophages. It is also present in the mitochondria and chloroplasts of eukaryotes, supporting the hypothesis that they are derived from prokaryotes.

formylmethionine deformylase EC 3.5.1.31; *systematic name*: *N*-formyl-L-methionine amidohydrolase; *other name*: **polypeptide deformylase**; an enzyme, found in prokaryotes, that removes the formyl group from the N-terminal *N*-formylmethionine of many polypeptides produced by translation of mRNA; example from *Escherichia coli*: DEF_ECOLI, 169 amino acids (19.33 kDa). *See also* **post-translational modification**.

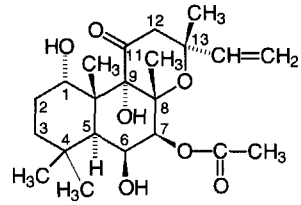
5-formyltetrahydrofolate *see* **folinic acid**.

5-formyltetrahydrofolate cyclo-ligase EC 6.3.3.2; *other name*: 5,10-methenyltetrahydrofolate synthetase; an enzyme that catalyses the reaction between ATP and 5-formyltetrahydrofolate to form 5,10-methylenetetrahydrofolate with release of ADP and orthophosphate.

formyltetrahydrofolate synthetase *see* **formate–tetrahydrofolate ligase**.

5-formyltetrahydrofolic acid *an alternative name for* **folinic acid**.

forskolin colforsin; 7β-acetoxy-8,13-epoxy-1α,6β,9α-trihydroxylabd-14-en-11-one; a diterpene isolated from the roots of the Indian labiate plant *Coleus forskohlii*. It stimulates adenylate cyclase, has positive inotropic activity, and relaxes smooth muscle; at higher doses it is hypotensive and vasodilatory. The water-solubility of the active 7-*O*-hemisuccinyl-7-deacetyl- or (less potent) 7-deacetyl-6-(*N*-acetylglycyl)- derivatives is useful; the 1,9-dideoxy-derivative is inactive and can be used as a control.



Forssman antibody an antibody against **Forssman antigen**; it causes agglutination of sheep erythrocytes.

Forssman antigen *or* **Forssman hapten** *abbr.*: F antigen; a heterophil antigen, present on the tissue cells of many species, including horse, sheep, and mouse, but absent in human and rabbit. The glycolipid hapten (from horse) is a ceramide pentasaccharide, GalNAc(α1-3)GalNAc(β1-3)Gal(α1-4)Gal(β1-4)Glc(β1-1)Cer; when incorporated in liposomes the nonpolar ceramide end anchors the hapten in the bilayer leaving the polar pentasaccharide region accessible to Forssman antibodies.

Förster theory of fluorescence energy transfer a theory giving the rate of dipole–dipole energy transfer in fluorescence as:

$$k_T = 8.71 \times 10^{23}(r^{-6}K^2Jn^{-4}k_F)$$

and the efficiency of transfer as:

$$E = r^{-6}/(r^{-6} + R_0^{-6}),$$

where R_0, the distance at which transfer efficiency is 50%, is given by:

$$R_0 = 9.71 \times 10^3\,(JK^2Q_0\,n^{-4})^{1/6}\text{Å},$$

in which r is the distance between the centres of donor and acceptor chromophore, K^2 is the orientation factor for a dipole–dipole interaction, J is the spectral overlap integral, n is the refractive index of the medium between the donor and acceptor, k_F is the rate constant for fluorescence emission by the energy donor, and Q_0 is the quantum yield of fluorescence of the energy donor in the absence of the acceptor. For energy transfer to be efficient the fluorescence emission spectrum of the donor must overlap the absorption spectrum of the acceptor, i.e. the donor and acceptor must be in resonance, as measured by the spectral overlap integral J, which, in $cm^3\ M^{-1}$, is:

$$J = (\int F(\lambda)\varepsilon(\lambda)\lambda^4 d\lambda)/(\int F(\lambda)d\lambda),$$

where $F(\lambda)$ is the fluorescence intensity in arbitrary units of the energy donor at wavelength λ in cm, and $\varepsilon(\lambda)$ is the extinction coefficient of the energy acceptor in $cm^{-1}\ M^{-1}$. The orientation factor, K^2, is given by:

$$K^2 = (\cos\alpha - 3\cos\beta\cos\gamma)^2,$$

where α is the angle between the donor and acceptor transition moments and β and γ are the angles between the donor moment and the acceptor moment and the line joining the cen-

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tres of the donor and acceptor, respectively. [After T. Förster.]

Förster transfer the nonradiative, resonant energy transfer that occurs when electronic excitation of one chromophore in a molecule, or other structure, elicits fluorescence from a different chromophore located up to 5–7 nm distant. For example, excitation of a tyrosine residue in a protein molecule can lead to fluorescence from a tryptophan residue in the same protein, and excitation of a tryptophan residue can cause fluorescence of dyes attached to the protein surface or to an embedded coenzyme. Resonant energy transfer is important in photosynthesis; many of the chlorophyll molecules in a chloroplast transfer the energy they have absorbed to other chlorophyll molecules at reaction centres.

fortimycin any of several aminoglycoside antibiotics from the actinomycete *Micromonospora olivoasterospora*.

FORTRAN *abbr. for* formula translator; a high-level computer language much used in numerical applications and engineering and the development of structure refinement software in structural molecular biology.

forward mutation any gene mutation from wild-type to the mutant phenotype, as opposed to a **back mutation**.

forward scattering scattering of radiation in the direction of the beam of radiation, i.e. away from the radiation source.

FOS a gene family encoding nuclear transcription factors; v-*fos* is the oncogene of the FBJ and FBR murine osteosarcoma viruses and Fujinami (avian) sarcoma virus. *FOS* is rapidly (within 5 minutes) but transiently expressed following stimulation of cells by mitogens and also during the onset of differentiation and by wounding. The gene product, FOS, and JUN (from the related gene family *JUN*) form homo- and heterodimers that bind to DNA; the heterodimers bind to the AP-1 consensus site (*see* ***JUN***); FOS homodimers bind to the TPA response element (TRE) if Glu^{168} is substituted by Lys. The proteins are members of the **leucine zipper** and **helix-turn helix** superfamilies; five motifs; database code FOS_HUMAN, 380 amino acids (40.65 kDa).

fosfomycin *another name for* **phosphonomycin**.

Fouchet's test a colour test for the presence of bilirubin in the urine. A green colour is produced when the sample is treated with iron (III) chloride solution and trichloroacetic acid.

Fourier analysis the fitting of the terms of a **Fourier series** to a set of periodic data.

Fourier series the expression of any ordinary, single-valued (univalent) periodic function:

$$y = f(x) \qquad (1)$$

as the sum of an infinite number of sine waves of successively higher orders. Substituting $n\theta$ for x, to be appropriate to circular functions,

$$y = a_0 + a_1\cos\theta + a_2\cos 2\theta + a_3\cos 3\theta + \ldots + b_0 + b_1\sin\theta + b_2\sin 2\theta + b_3\sin 3\theta + \ldots \quad (2)$$

The coefficients a_n and b_n can be uniquely determined by equating equations (1) and (2) point by point for successive values of x and solving the simultaneous equations so found. [After Jean Baptiste Joseph Fourier (1768–1830), French mathematician.]

Fourier synthesis the process of computing the form of a function from the values of the coefficients of its **Fourier series**.

FP *abbr. for* flavoprotein.

F6P *abbr. for* fructose 6-phosphate.

F-pilus a type of sex pilus, one or two of which may be present in each cell of 'male' strains of *Escherichia coli*. Each pilus is approximately 8 nm in diameter and up to 20 μm long. F-pili are consistently associated with the presence in the bacterium of the **F′ plasmid**, which directs their synthesis; they are believed to serve as conductors of nucleic acids in various circumstances, e.g. during bacterial conjugation.

F plasmid *or* **F factor** the prototype 'fertility factor' responsible for conjugation in the K-12 strains of *Escherichia coli* used in the early studies of bacterial mating. The letter F refers specifically to this plasmid and thus should not be used to refer to other naturally occurring **conjugative plasmids**.

F′ plasmid *or* **F′ factor** an **F plasmid** derivative incorporating a segment of the bacterial chromosome. An organism in which an F′ plasmid has arisen and that carries a chromosomal deletion corresponding to the segment incorporated by the plasmid is termed a **primary F′-containing strain**, and an organism into which an F′ plasmid has been transferred is termed a **secondary F′-containing strain**.

FPS *see* ***FES/FPS***.

Fr *symbol for* francium.

fraction **1** *(in chemistry)* any one of several portions of a mixture that can be separated by a fractional process, e.g. by fractional distillation or chromatography, and consisting either of a mixture or of a pure compound. **2** to separate or divide into portions; to **fractionate**.

fraction I–VI (of blood plasma) *see* **Cohn fractionation**.

fractional **1** of, relating to, or being a fraction. **2** of or denoting any process by which parts of a mixture are separated by exploiting differences in their physical properties, e.g. their boiling points, solubility, or chromatographic characteristics.

fractional centrifugation *an alternative name for* **differential centrifugation**.

fractional crystallization the separation of substances with nearly the same solubilities. It involves a series of recrystallizations at each stage of which the crystals will be enriched in one component and the mother liquor will be enriched in the other component.

fractional distillation the process of separating the components of a mixture by heating it and separately condensing portions of vapour at different temperatures, corresponding to the boiling points of the components of the mixture.

fractional precipitation the stepwise separation of substances, especially macromolecules, from a solution by exploiting differences in their solubilities in various conditions of pH, ionic strength, dielectric constant, etc. Changes in these conditions are effected by the addition of acid, alkali, salt (e.g. ammonium sulfate), ethanol, or other substances.

fractional sterilization *an alternative name for* **tyndallization**.

fractionate **1** to separate (a mixture) or cause (a mixture) to separate into portions or fractions, e.g. by distillation or crystallization. **2** to obtain (a part of a mixture) by a **fractional** process. —**fractionation** *n.*

fractionating column a vertical tube or hollow column frequently forming part of an apparatus for **fractional distillation** and usually filled with packing or intersected with perforated plates. An internal reflux takes place during distillation resulting in a gradual separation between the high-boiling-point fractions and the low-boiling-point fractions, the lowest-boiling-point fraction distilling over first.

fraction collector *or (sometimes)* **fraction cutter** an apparatus for the automatic collection of consecutive, commonly equal-sized, fractions of a flowing liquid, e.g. of the eluate from a chromatographic column. The size of the fractions may be predetermined by volume, mass, time, or number of drops.

fraction cutter **1** the device in a **fraction collector** that separates the flow of eluate into fractions of predetermined size, which then may be individually collected. **2** *(sometimes) an alternative name for* **fraction collector**.

fraction I protein *a former name for* RuBP carboxylase; *see* **ribulose bisphosphate carboxylase**.

fragile X syndrome an X-linked inherited disorder, with mental retardation and connective tissue abnormalities, arising from a **trinucleotide repeat** of CGG.

fragment-antigen binding *see* **Fab fragment**.

fragmentation **1** *(in cell biology)* **a** the separation of a small piece (i.e. a fragment) of a chromosome from the rest. **b** the division of a cell nucleus by simple splitting. **2** *(in chemistry)* the breakdown of a radical into a diamagnetic molecule and a smaller radical; the breakdown of a radical ion in a mass

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spectrometer to form an ion of lower molecular mass and a radical.

fragment-crystallizable *see* **Fc fragment**.

fragment ion *(in mass spectrometry)* any ion produced by the loss of one or more pieces from a parent **molecular ion** (or larger fragment ion).

fragmentography *see* **molecular fragmentography**.

fragmin a Ca^{2+}-sensitive protein, of M_r 43 000 and isolated from *Physarum polycephalum*, that regulates the length of actin filaments *in vitro*.

frame *short name for* **reading frame**.

frameshifting *(in ribosomal function) see* **programmed ribosomal frameshifting**.

frameshift mutagen any mutagen that is capable of causing **frameshift mutations**.

frameshift mutation *or* **phaseshift mutation** any mutation involving the addition or deletion of nucleotide residues in a DNA molecule that results in out-of-phase translation, at positions beyond the site of mutation, of the messenger RNA formed from it. Since the genetic code is read as unpunctuated base triplets, additions or deletions in the message that are not multiples of three bases result in a shift in the reading frame.

frameshift suppressor any of a class of external suppressor mutations that specifically suppress a frameshift mutation by changing (correcting) the phase of translation. Frameshift suppressors are genetic alterations outside the mutated cistron. Some give rise to altered tRNA molecules, **frameshift suppressor tRNAs**, that recognize a base quadruplet instead of a base triplet.

Franck, James (1882–1964) German-born US physicist notable for his work on quantum theory (with G. Hertz), on photochemistry (e.g. the Franck–Condon principle), and on the development of atomic energy (but in opposing the use of nuclear weapons); Nobel Laureate in Physics (1925) jointly with G. Hertz 'for their discovery of the laws governing the impact of an electron upon an atom'.

Franck–Condon principle the principle that the time taken for electronic transitions in molecules is very short in comparison with the period of vibration of the atomic nuclei, with the consequence that the nuclei do not appreciably alter their positions during the emission or absorption of a photon. [After J. **Franck** and Edward Uhler Condon (1902–74), US physicists.]

Frank, Il'ja Mikhailovich (1908–1990), Russian-born Soviet physicist noted for establishing the theoretical basis of the *Cherenkov effect*; Nobel Laureate in Physics (1958) jointly with P. A. Cherenkov and I. Y. Tamm 'for the discovery and interpretation of the Cherenkov effect'.

Franklin, Rosalind Elsie (1920–58) British biophysicist, who obtained X-ray data for DNA that were consistent with and provided insight that contributed to the proposal of a helical structure published by J. D. Watson and F. H. C. Crick.

FRAT *abbr. and proprietary name for* free radical assay technique (*see* **spin immunoassay**).

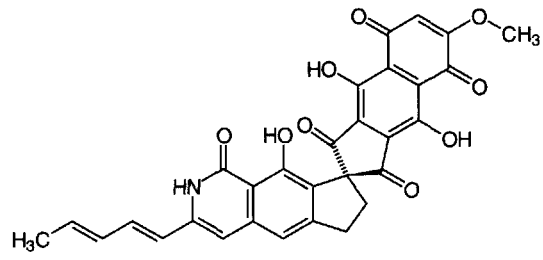
frataxin a 210-residue protein identified from a mutation found in **Friedreich's ataxia** (*abbr.*: FRDA). Some FRDA patients have point mutations in the gene encoding frataxin, but the majority are homozygous for an unstable GAA trinucleotide expansion in the first intron. The function of the protein is unknown.

fraudulent DNA a DNA molecule containing **fraudulent nucleotides**.

fraudulent nucleotide any (artificial) nucleotide that contains a non-naturally occurring base that is an analogue of a purine or pyrimidine found in natural DNA.

frayed end (of DNA) an end region of a double-stranded polynucleotide in which there is imperfect complementarity of the base pairs.

fredericamycin A an antibiotic produced by *Streptomyces griseus* that contains a *spiro* ring system and is active against Gram-positive bacteria and fungi. It is cytotoxic against some transplantable tumours.



fredericamycin A

free *(in chemistry)* not chemically combined (with another substance); not physically bound (to another substance).

free diffusion diffusion in a gas phase or across a boundary between two solutions (or between a solution and pure solvent), as distinct from diffusion across a membrane or some other porous barrier.

free-draining coil a model for polymer molecules in solution that are not well approximated by a solid particle. In this model the polymer is considered as a string of beads through which the solvent streams during viscous flow.

free electrophoresis *an alternative name for* **moving boundary electrophoresis** (def. 1).

free energy *an alternative name for* **Gibbs energy**.

free energy change *an alternative name for* **Gibbs free energy change**.

free fatty acid *abbr.*: FFA; a nonesterified fatty acid; the term is often used of such acids in the blood.

free-flow electrophoresis *an alternative name for* **moving boundary electrophoresis** (def. 1).

free radical *see* **radical** (def. 1).

free-radical scavenger *the former term for* **radical scavenger**.

free rotation sterically unhindered rotation of atoms or groups about a single covalent bond.

freeze-clamp to halt abruptly the metabolic processes in a piece of tissue, or other specimen, by clamping it into a thin, frozen wafer between two aluminium (or other metal) plates, previously cooled in liquid nitrogen. The frozen specimen then may be pulverized and treated with a protein precipitant, e.g. acetone at –70 °C. The technique is useful in the determination of the concentrations of various metabolites that otherwise are rapidly consumed by enzymic action continuing during an investigation.

freeze-cleaving *an alternative term for* **freeze-fracturing**; *see also* **freeze-etching**.

freeze-dry to dry in a frozen state at very low pressure (i.e. in a high vacuum) so that ice, or other frozen solvent, sublimes rapidly, leaving a porous solid; to lyophilize. Used, e.g. in histochemistry, as frozen biological material can be preserved by removal of water under vacuum without damage to cell structures.

freeze-dryer any apparatus used for freeze-drying.

freeze-etching *or* **frozen replica method** a technique of preparing, for electron-microscopic examination, a surface that has been exposed by fracturing or cutting a deep-frozen specimen. The sample is rapidly frozen to about –150 °C and placed in a vacuum, where it is cleaved or sliced with a cold knife – the process known as **freeze-fracturing**. Etching is then achieved by evaporation of some of the solvent from the surface in a vacuum at about –100 °C to produce a textured field, in which nonvolatile macromolecules protrude from a frozen aqueous layer. A replica of the surface is then prepared by shadowing with carbon and/or a heavy metal while the sample is still in the vacuum. This replica is then lifted off, rinsed, and placed

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on an electron microscope grid for examination. *See also* **replica formation**.

freeze-fracturing *(in electron microscopy)* a method of visualizing the interior of cell membranes in which cells are frozen at the temperature of liquid nitrogen in the presence of antifreeze and then the frozen block is cracked with a knife blade. The fracture plane often passes through the hydrophobic middle of lipid bilayers, thereby exposing the interior of cell membranes. The resulting fracture faces are shadowed with platinum, the organic material is dissolved away and the replicas floated off for electron microscopy.

freeze-stop to stop a reaction rapidly by freezing the reaction mixture; to **freeze-clamp**.

freeze–thaw to disrupt cells in a suspension, or to disperse emulsions, by repeated freezing and thawing.

freezing **1** the change of a liquid into a solid by a lowering of temperature. **2** the stopping of a reaction or other process at a particular point, often by a lowering of temperature. **3** *or* **cryopreservation** the use of temperatures below 0 °C in order to preserve biochemicals and foodstuffs, or to maintain viable populations of (micro)organisms.

freezing-microtome a microtome in which the tissue sample is frozen and maintained in a frozen state with liquid carbon dioxide. It is useful for (rapidly) obtaining sections of unfixed soft tissue. *Compare* **cryomicrotome**.

freezing point the temperature at which **freezing** (def. 1) occurs.

French chalk *see* **talc**.

French pressure cell a device to disrupt chloroplasts and bacteria, yeasts, or other cells. A cell or chloroplast suspension is placed in a cylinder fitted with a piston and a narrow outlet controlled by a needle valve. After removal of air, the piston is forced into the cylinder with a hydraulic press to the desired operating pressure (<20 000 pound-force per square inch, 140 MPa). The valve is then opened. Extrusion through the narrow orifice together with the sudden release of pressure creates shear forces that break the suspended particles. *See also* **Hughes press**. [After Charles Stacy French (1907–), US plant physiologist.]

Freon *the proprietary name for* any of a group of fluorocarbon or chlorofluorocarbon compounds that are clear, colourless liquids, chemically inert, and of low toxicity. They are useful as refrigerants, aerosol propellants, cleaning fluids, and solvents. These substances have been shown to be important in the chemical removal of ozone by chlorine-catalysed cycles in the polar region during winter and spring. Nitric oxide and ice-clouds are formed in the polar stratosphere during winter. Heterogeneous chemical reactions take place on the surface of these particles, dramatically shifting the balance between inactive and active forms of chlorine and increasing the efficiency of chlorine in catalytic ozone removal. The use of Freon is being phased out in many countries; it is being replaced by substances such as tetrafluoroethane (ICI Trademark KLEA) which are claimed not to cause depletion of ozone.

frequency *symbol*: ν *or* f; the number of complete cycles of any periodic process occurring in unit time. The SI derived unit of frequency is the **hertz**. The frequency of a wave is equal to its velocity divided by its wavelength.

frequency distribution a table, graph, or histogram constructed from a series of measurements to show the classes into which the measurements are divided and the numbers in each of these classes.

fresnel a non-SI unit of frequency of electromagnetic radiation, equal to 10^{12} Hz.

Fresnel diffraction the diffraction occurring when electromagnetic radiation encounters abrupt discontinuities in refractive index, as in a **Fresnel lens** or in the examination of some specimens in (electron) microscopy. [After Augustin Jean Fresnel (1788–1827), French physicist.]

Fresnel lens a lens whose surface consists of a concentric series of lens sections (or one convex surface and one stepped surface). This arrangement allows a thin lens of short focal length and large diameter to be easily made, and finds application in searchlights, viewing devices, and overhead projectors.

fret a broad membrane-bound channel interconnecting the grana of **chloroplasts**.

Freund's adjuvant a widely used immunological **adjuvant** (def. 1), used to produce water-in-oil emulsions with aqueous antigens or antigen preparations. It consists of a mixture of mineral oil and emulsifier (**incomplete Freund's adjuvant**) in which killed mycobacteria have been dispersed (**complete Freund's adjuvant**). Omission of mycobacteria may modify the duration, intensity, and nature of the responses. [After Jules Freund (1891–1960).]

Frey–Wyssling particle a double-membrane particle (4–6 μm in diameter) representing a minor component of rubber latex. [After Albert Frey-Wyssling (1900–).]

FRF *abbr. for* follicle-stimulating-hormone-releasing factor; *see* **gonadotropin-releasing hormone**.

FRH *abbr. for* follicle-stimulating hormone releasing hormone; *see* **gonadotropin-releasing hormone**.

friable easily crumbled or pulverized.

friction the resistance to the relative motion of one body sliding, rolling, or flowing over another body with which it is in contact. —**frictional** *adj.*

frictional coefficient *or* **frictional constant** *symbol*: f; the frictional force opposing the motion of a body in a fluid medium divided by the velocity of movement. It may be expressed in different ways. The **translational frictional coefficient**, f, for a rigid sphere of radius r moving at low velocity through a medium of viscosity η, is given by: $f = 6\pi\eta r$ (**Stokes' law of viscosity**). For particles of other shapes additional terms must be included. The **rotational frictional coefficient**, f_{rot}, is a parameter relating the velocity of rotation of a rigid sphere of volume V in a fluid medium of viscosity η. It is given by: $f_{rot} = 6\eta V$. *See also* **frictional ratio**.

frictional force the force exerted on a particle moving through a fluid medium as a result of friction. It is the product of the velocity, relative to the medium, of the particle and its **frictional coefficient**.

frictional ratio the ratio of the experimentally determined translational **frictional coefficient**, f, of a hydrated, anisotropic macromolecule to the calculated frictional coefficient, f_0, of a nonhydrated spherical macromolecule of the same molecular mass. The ratio f/f_0 gives some indication of the asymmetry of the macromolecule.

Friedreich's ataxia an autosomal recessive inherited disease that involves the central and peripheral nervous systems and the heart. It is the most common hereditary ataxia, and is associated with defects in the gene encoding **frataxin**.

Friend cell a cell of a cultured cell line of leukemic mouse erythroblasts obtained by transformation with Friend leukemia virus. In such cells development is arrested before any globin synthesis occurs, but treatment with certain chemicals, e.g. dimethylsulfoxide, causes a resumption of development and hemoglobin synthesis.

Friend leukemia virus a strain of mouse type C oncovirus that specifically affects immature erythroid cells in mice to cause an erythroleukemia. [After Charlotte Friend (1921–).]

frit filter *or* **fritted filter** *or* **fritted glass filter** *an alternative name for* **sintered glass** filter.

Fromm's method a kinetic approach for studying the mechanism of action of enzyme systems that utilize three substrates. Such systems may be divided into two groups on the basis of their initial rate expressions: the first group is made up of sequential pathways of enzyme and substrate interaction alone, the second is the ping-pong type. The mechanisms in each category may further be separated either by initial rate measurements or from studies with competitive inhibitors. [After Herbert Jerome Fromm (1929–), US biochemist.]

frontal analysis any analytical technique by which the progress of the separation of components of a mixture, as by

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frontal chromatography, moving boundary electrophoresis, or analytical ultracentrifugation, is followed, and the relative proportions of the components determined, by examination of the individual boundaries, or fronts, formed by each component with the solvent.

frontal chromatography a technique for chromatographic separation in which the sample (liquid or gas) is fed continuously into the chromatographic bed and only the component that emerges first is obtained in pure form.

fronting *(in chromatography)* the asymmetry of a peak such that, relative to the baseline, the front is less steep than the rear. In paper chromatography and thin-layer chromatography it refers to the distortion of a zone showing a diffuse region preceding the zone in the direction of flow.

frontside attack the mechanism of a chemical displacement reaction in which the configuration is retained.

frozen replica method *an alternative name for* **freeze-etching**.

FRS *abbr. for* Fellow of the Royal Society (of London).

FRSE *abbr. for* Fellow of the Royal Society of Edinburgh.

Fru *symbol for* a residue (or sometimes a molecule) of the ketohexose **fructose**. In the condensed system of symbolism of sugar residues, Fru signifies specifically a fructose residue with the common configuration and ring size, i.e. D-fructofuranose.

fructan any **glycan** composed only of D-fructose residues. Fructans occur commonly as food reserves in the roots, stems, leaves, and seeds of many plants, e.g. in tubers of dahlias and Jerusalem artichokes. There are two main types: (1) inulin-type, in which the fructofuranose residues are linked by $\beta 2 \rightarrow 1$ glycosidic linkages; and (2) levan-type, in which the linkages are $\beta 2 \rightarrow 6$, which were formerly referred to as **fructosans**.

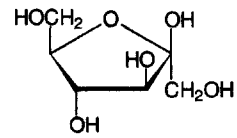
β-fructofuranosidase EC 3.2.1.26; *other names*: invertase; saccharase; an enzyme that catalyses the hydrolysis of terminal nonreducing β-D-fructofuranoside residues in β-D-fructofuranosides, e.g. sucrose. Examples: precursors of invertases types 1, 2 and 4 from yeast: database code INV1_ YEAST, 532 amino acids (60.50 kDa); INV2_YEAST, 532 amino acids (60.57 kDa); INV4_ YEAST, 532 amino acids (60.51 kDa).

fructokinase **1** *the recommended name for* the enzyme ATP:D-fructose 6-phosphotransferase; EC 2.7.1.4; this catalyses the phosphorylation of D-fructose by ATP to form D-fructose 6-phosphate and ADP. The enzyme occurs in plants and in schistosomes, and is highly specific for D-fructose. In bacteria it is important in fructose utilization. Structurally it is similar to other carbohydrate kinases. Example from *Zymomonas mobilis*: database code SCRK_ZYMMO, 301 amino acids (32.57 kDa). **2** *an alternative name for* **ketohexokinase** (EC 2.7.1.3). This usage is misleading since ketohexokinase yields D-fructose 1-phosphate.

fructosaccharase *a trivial name for* any **saccharase** that attacks the fructose-containing end of appropriate oligosaccharides, liberating fructose.

fructosan **1** *(formerly) a trivial name for* 2,6-anhydrofructofuranose. **2** *an (older) incorrect name for* **fructan**.

fructose *symbol*: Fru; *the trivial name for* the ketohexose *arabino*-2-hexulose; there are two enantiomers. D-(−)-fructose (*symbol*: D-Fru), commonly known as fructose, and formerly known as **fruit sugar**, is levorotatory, hence formerly known also as **levulose** *or* (*esp. UK*) laevulose; it is the sweetest of the sugars. Aqueous solutions of D-fructose at room temperature contain an equilibrium mixture of β-D-fructopyranose, β-D-fructofuranose, α-D-fructofuranose, and the open-chain form, whereas in crystals the sugar is present entirely as β-D-fructopyranose. Combined D-fructose is almost invariably in the furanose form, however. D-fructose is found free in a large number of fruits, in honey, and (as the sole sugar) in bull and human semen. In combined form it occurs at one residue per molecule of the disaccharide **sucrose** and the trisaccharides **gentianose**, **melezitose**, and **raffinose**, and as the sole component of the polysaccharide **fructans**.



β-D-fructofuranose

fructose-bisphosphatase EC 3.1.3.11; *systematic name*: D-fructose-1,6-bisphosphate 1-phosphohydrolase; *other names*: hexosediphosphatase; *(formerly)* fructose-1,6-diphosphatase. A phosphoric monoester hydrolase that hydrolyses D-fructose 1,6-bisphosphate to D-fructose 6-phosphate and orthophosphate. It is important in **gluconeogenesis** and in regulation of the **reductive pentose phosphate cycle** in chloroplasts. Example from rat: database code F16P_RAT, 362 amino acids (39.43 kDa); six motifs.

fructose-2,6-bisphosphatase an enzyme that hydrolyses fructose 2,6-bisphosphate to fructose 6-phosphate; it is the same protein as phosphofructokinase-2. *See* **phosphofructokinase** (def. 2).

fructose-1,6-bisphosphatase deficiency *see* **hereditary fructose-1,6-bisphosphatase deficiency**.

fructose 1,6-bisphosphate *or (formerly)* **fructose 1,6-diphosphate** *abbr.*: FBP; the D enantiomer is a metabolic intermediate in **glycolysis** and **gluconeogenesis**.

fructose 2,6-bisphosphate the D enantiomer is an important regulator of the **glycolytic** and **gluconeogenic pathways**. It inhibits fructose 1,6-bisphosphatase and activates phosphofructokinase, and its concentration is controlled by the **phosphofructokinase** (def. 2) and fructose 2,6-bisphosphatase activities of a 49 kDa protein.

fructose-bisphosphate aldolase EC 4.1.2.13; *systematic name*: D-fructose-1,6-bisphosphate D-glyceraldehyde-3-phosphate lyase; *other names*: aldolase; fructose-1,6-bisphosphate triosephosphate-lyase. An enzyme that catalyses the reaction:

D-fructose 1,6-bisphosphate = glycerone phosphate + D-glyceraldehyde 3-phosphate.

It is a universally distributed enzyme that functions in the pathways for both the catabolism and biosynthesis of glucose. Example from *Drosophila melanogaster*: database code NRL_1FBAA, 360 amino acids (38.87 kDa); 3-D structure known.

fructose-2,6-bisphosphate 2-phosphatase EC 3.1.3.46; *other name*: fructose-2,6-bisphosphatase; an enzyme that catalyses the hydrolysis of D-fructose 2,6-bisphosphate to D-fructose 6-phosphate and orthophosphate, being part of the system for regulating the concentration of fructose 2,6-bisphosphate. This enzyme is the phosphorylated form of the protein. If dephosphorylated, it functions as a 2-kinase for fructose 6-phosphate. Example, human liver isoform: database code F26L_HUMAN, 471 amino acids (54.64 kDa). *See also* **phosphofructokinase** (def. 2).

fructose-1,6-diphosphatase *a former name for* **fructose-bisphosphatase**.

fructose 1,6-diphosphate *a former name for* **fructose 1,6-bisphosphate**.

fructose disease *see* **essential fructosuria**, **hereditary fructose intolerance**, **hereditary fructose-bisphosphatase deficiency**.

fructose intolerance *an alternative name for* **essential fructosuria**.

fructose 6-phosphate *abbr.*: F6P; the D enantiomer is an important intermediate in glycolysis, gluconeogenesis, and fructose metabolism.

fructosuria the presence of abnormal amounts of fructose in the urine. *See also* **essential fructosuria**.

Fru*f* *symbol for* a fructofuranose residue.

fruit the structure that develops from the fertilized ovary of a

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flowering plant and contains the ripening seed or seeds. It may be fleshy or dry; the term is often extended to include other associated parts such as a fleshy receptacle.

fruit fly a common name for species of flies belonging to the genus *Drosophila*.

fruit-ripening hormone *see* **ethylene**.

fruit sugar *a former name for* the D enantiomer of **fructose**.

FSF *abbr. for* fibrin-stabilizing factor (i.e. factor XIIIa); *see* **blood coagulation**.

FSH *abbr. for* follicle-stimulating hormone.

FSH-RF *abbr. for* follicle-stimulating hormone releasing factor; *see* **gonadotropin-releasing hormone**.

FSH-RH *abbr. for* follicle-stimulating hormone releasing hormone; *see* **gonadotropin-releasing hormone**.

F_1 sphere a submitochondrial structure containing the catalytic site for ATP synthesis.

F′-strain a bacterial strain containing an **F′ plasmid**.

F-type pentose phosphate pathway *see* **pentose phosphate pathway**.

ftz the gene for Fushi Tazaru protein, a nuclear DNA-binding homeobox segmentation protein from *Drosophila melanogaster*. Database code HMFT_DROME, 413 amino acids (46.82 kDa).

FU *abbr. for* fluorouracil (use proscribed; the symbol FUra is recommended).

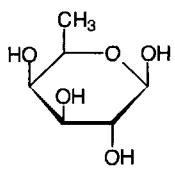
Fuc *symbol for* a residue (or sometimes a molecule) of the deoxyaldohexose **fucose**. In the condensed system of symbolism of sugar residues, Fuc signifies specifically a fucose residue with the common configuration and ring size, i.e. L-fucopyranose.

fucan a **glycan** composed only of fucose residues.

fucoidan *or* **fucoidin** any of a group of complex branched, sulfated heteropolysaccharides that are composed of residues of L-fucose (usually sulfated) together with small numbers of residues of various other monosaccharides. Fucoidans occur in the cell walls, intercellular matrix, and exuded mucilage of many (especially intertidal) species of marine algae, in which they appear to assist in water retention during periodic exposure.

fucosamine 2-amino-2,6-dideoxygalactose; an aminodeoxysugar, both enantiomers of which occur in lipopolysaccharides of *Salmonella* and other bacterial genera.

fucose *symbol*: Fuc; *the trivial name for* 6-deoxygalactose; there are two enantiomers. **D-Fucose** (*symbol*: D-Fuc), 6-deoxy-D-galactose, occurs in glycosides in various plants belonging to the Convolvulaceae. **L-Fucose** (*symbol*: L-Fuc), 6-deoxy-L-galactose, occurs in polysaccharides (fucans) in seaweeds, especially *Fucus* spp., and in the cell wall matrix of higher plants. In animals fucosyl residues occur in a number of glycoproteins and glycolipids; the presence of α-1,4-linked L-fucosyl residues at specific positions in the highly branched oligosaccharides of human erythrocyte surface antigens is controlled by the *H* and *Le* blood-group genes.



β-D-fucose

fucose-1-phosphate guanylyltransferase EC 2.7.7.30; *other name*: GDPfucosepyrophosphorylase; an enzyme that catalyses the formation of GDP-L-fucose from GTP and L-fucose 1-phosphate with release of pyrophosphate.

α-fucosidase any of several enzymes that hydrolyse α-fucosides. **1** α-fucosidase, EC 3.2.1.51; *systematic name*: α-L-fucoside fucohydrolase; it catalyses the hydrolysis of an α-L-fucoside to an alcohol and L-fucose. Example from human: database code FUCO_HUMAN, 461 amino acids (53.10 kDa). **2** 1,3-α-L-fucosidase, EC 3.2.1.111; *other names*: almond emulsin; fucosidase I; an enzyme that catalyses the hydrolysis of 1,3-linkages between α-L-fucose and *N*-acetylglucosamine residues in glycoproteins. **3** 1,6-α-L-fucosidase, EC 3.2.1.127; an enzyme that catalyses the hydrolysis of 1,6-linkages between α-L-fucose and *N*-acetyl-D-glucosamine in glycopeptides such as immunoglobulin G glycopeptide and fucosyl-asialo-agalacto-fetuin.

fucosidosis an inherited human metabolic disorder in which there is an inability to remove α-L-fucosyl residues from various glycoproteins and glycolipids. It is subject to autosomal recessive inheritance.

FUdR *or* **FUDR** *abbr. for* fluorodeoxyuridine (use deprecated; the symbol FdUrd is recommended).

fugu toxin *see* **tetrodotoxin**.

full agonist an **agonist** that is able to elicit the maximal response of a tissue even when the tissue has spare receptors. In such a situation, several different agonists may be able to elicit the same maximal response, albeit at different receptor occupancies. Moreover, a full agonist in one tissue may be a **partial agonist** in another.

fuller's earth a naturally occurring, porous, absorptive aluminium–magnesium silicate clay. It is useful for decolorizing oils and other liquids and as a filtering medium. It is so-called because it was originally used to full (i.e. cleanse and thicken) wool and woollen cloth.

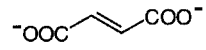
fully overlapping code *see* **overlapping code**.

fumarase EC 4.2.1.2; *recommended name*: fumarate hydratase. An enzyme of the **tricarboxylic-acid cycle** that catalyses the reaction:

$$(S)\text{-malate} = \text{fumarate} + H_2O.$$

There are two different enzymes in facultative bacteria (e.g. *Escherichia coli*). Example human mitochondrial enzyme, homotetramer: database code FUMH_HUMAN, 467 amino acids (50.20 kDa).

fumarate **1** *the trivial name for trans*-1,2-ethylenedicarboxylate, (*E*)-butenedioate, the dianion of fumaric acid; the diastereoisomer of **maleate** and a key intermediate in metabolism. In the tricarboxylic-acid cycle it is formed from succinate by **succinate dehydrogenase**, and is converted to malate by **fumarase**. **2** any mixture of fumaric acid and its mono- and dianions. **3** any salt or ester of fumaric acid.



fumarate hydratase *see* **fumarase**.

fumaroyl the bivalent *trans*-acyl group, –CO–CH=CH–CO–, derived from fumaric acid.

fumaryl the univalent *trans*-acyl group, HOOC–CH=CH–CO–, derived from fumaric acid.

fumed silica a preparation of pure silicon dioxide as an extremely fine, white powder with an external surface area of up to 400 $m^2 g^{-1}$. It is useful for thickening and forming thixotropic gels. Fumed silica is used as a suspending and gelling agent in liquid-scintillation counting; a 3–5% concentration in dioxan, toluene, or xylene-based liquid scintillators will form an almost transparent, rigid gel, capable of holding an insoluble solid sample in suspension. *Proprietary name*: Cab-O-Sil.

fume hood a work space contained under a hood from which air is extracted to remove harmful vapours.

function **1** *(in chemistry)* a **functional group**. **2** *(in mathematics)* **a** either of two variables so related to each other that for any value of one variable there is a corresponding value of the other. **b** a variable or expression that can take a set of values

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each of which is associated with the magnitude of an independent variable or variables. **3** *(in physiology)* the normal vital activity of a cell, organ, or tissue within an organism. —**functional** *adj.*

functional antagonism **1** antagonism arising by the antagonist's producing an opposite effect to the substance being antagonized through the antagonist's action at a different receptor. **2** antagonism arising when the antagonist interferes with events that follow receptor activation by the substance being antagonized.

functional cloning a cloning strategy in which knowledge of a gene's product (function) is used to clone the gene. An example is the gene for the β chain of hemoglobin responsible for sickle-cell anemia. This is in contrast to **structural cloning** where the function of the gene is not known. A common procedure would be to construct a DNA oligonucleotide based on the amino-acid sequence of the peptide and use this as a probe to isolate the gene from a DNA library. In cases where one protein is dominant in a cell, such as hemoglobin in the reticulocyte, the preparation of a cDNA from the mRNA also provides a useful probe for gene isolation.

functional group *or* **function** *(in chemistry)* any **group** (def. 1) in a molecule of an organic compound that confers characteristic chemical and physical properties on the molecule and that may be considered to have replaced a hydrogen atom in a molecule of the corresponding hydrocarbon, e.g. the hydroxyl group in an alcohol.

fungicide any biological, chemical, or physical agent able to destroy fungi. —**fungicidal** *adj.*

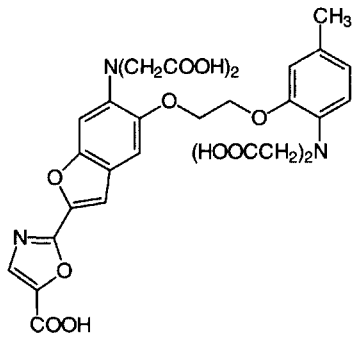
fungistat any drug, antibiotic, or other agent that inhibits the growth and multiplication of fungi. —**fungistatic** *adj.*

fungus (*pl.* **fungi**) any member of the taxonomic kingdom Fungi, a group of diverse and widespread unicellular, multicellular, or cenocytic eukaryotic organisms that do not contain chlorophyll. Fungi may be parasitic, saprophytic, or symbiotic. They reproduce through spores. *See also* **microfungus**. —**fungal** *adj.*

FUR *abbr. for* fluorouridine (use proscribed; the symbol FUrd is recommended).

FUra *symbol for* (a residue of) the synthetic pyrimidine base **fluorouracil**.

Fura 2 1-[2-(5-carboxyoxazol-2-yl)-6-aminobenzofuran-5-oxyl]-2-(2′-amino-5′-methylphenoxy)-ethane-*N*,*N*,*N*′,*N*′-tetraacetic acid; a highly sensitive calcium ion chelator that exhibits a spectral shift on binding Ca^{2+}. Calcium ion concentration can be measured directly, independent of dye concentration, by measuring the ratio of fluorescence at 510 nm after excitation at 340 nm and then at 380 nm. It is frequently used as the acetoxymethyl ester (Fura 2/AM, Fura 2-pentakis(acetoxymethyl)ester), which is a membrane-permeable derivative that can enter cells, after which it is rapidly hydrolysed by cytoplasmic esterases to Fura 2, which remains trapped within the cell and can thus report the intracellular Ca^{2+} concentration. *See also* **Quin-2**.



furan *the trivial name for* oxa-2,4-cyclopentadiene, C_4H_4O. *See also* **furanose**.

furanoid furan-like, i.e. describing a molecular structure that consists of or contains a ring of four carbon atoms and one oxygen atom (as in furan).

furanose *symbol*: *f*; any monosaccharide or monosaccharide derivative whose molecule contains a furanoid ring. *Compare* **pyranose**, **septanose**.

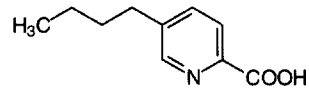
furanoside any glycoside in which the sugar moiety is in the furanose form.

FUrd *symbol for* (a residue of) the ribonucleoside fluorouridine (*see* **fluorouracil**).

furin the mammalian counterpart of **kexin**. Example from human: database code FURI_HUMAN, 794 amino acids (86.58 kDa).

furyl either 2-furyl or 3-furyl, the two oxa-2,4-cyclopentadienyl groups derived from a molecule of **furan** by loss of a hydrogen atom from C-2 and C-3 respectively.

fusaric acid 5-butylpyridine-2-carboxylic acid; an antibiotic originally isolated from the fungus *Fusarium heterosporium* and obtained also from *Gibberella fujikuroi*. It inhibits **dopamine β-hydroxylase** and has hypotensive activity.

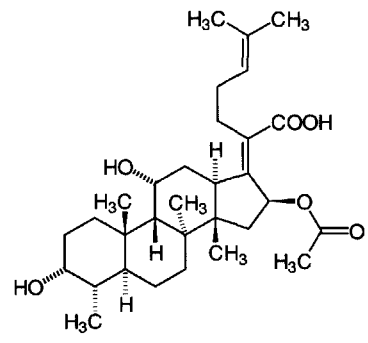


fused ring *(in chemistry)* any ring of atoms in a molecule that is joined to another ring of atoms in such a way that two atoms are common to both rings.

fused rocket immunoelectrophoresis a modification of **rocket immunoelectrophoresis** designed to follow the distribution of proteins among the fractions obtained in a separation experiment. Small volumes of fractions obtained in the separation experiment are placed in a row of sample wells in an antibody-free agarose gel and the samples are allowed to diffuse into the gel for 30–60 min. The proteins are then forced at right angles into an antibody-containing gel by electrophoresis; the resulting precipitation lines (rockets) show the elution profiles for each individual protein in the separation experiment and the distance between the precipitation line and the corresponding well is proportional to the amount of antigen precipitated.

fusel oil a colourless, oily liquid of variable composition obtained as a by-product in the distillation of alcoholic fermentation liquors. It contains chiefly isopentanol, 2-methyl-1-butanol, isobutanol, and propanol. It is considerably more toxic than ethanol. [From German *fuseln*, to bungle.]

fusidic acid 3α,11α,16β-trihydroxy-4α,8,14-trimethyl-18-nor-5α,8α,9β,13α,14β-cholesta-17(20),24-dien-21-oic acid 16-acetate; a steroid antibiotic, structurally related to cephalosporin P (*see* **cephalosporin**) and isolated from the fermentation broth of



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Fusidium coccineum. Fusidic acid is active particularly against Gram-positive organisms, especially *Staphylococcus* spp. It prevents translocation during protein synthesis and inhibits the accumulation of ppGpp.

fusiform spindle-shaped; elongated and tapering at both ends.

fusion **1** the act or process of melting. **2** the act or process of melting together or uniting. **3** the process whereby two membranes are joined together, as in **cell fusion**. **4** the process whereby nuclei of light elements are united to form nuclei of heavier elements with the release of energy: **nuclear fusion**. **5** the state of being fused. **6** something produced by fusion. **7** *(in molecular biology)* the act, process, or result of artificially linking genes that code for two different proteins, with the aim of generating a **fusion protein**.

fusion protein an expression product resulting from the fusion of two genes. Such a protein may be produced, e.g., in recombinant DNA expression studies or, naturally, in certain viral **oncogenes** in which the oncogene is fused to ***gag***. Their production sometimes results from the need to place a cloned eukaryotic gene under the control of a bacterial promoter for expression in a bacterial system; sequences of the bacterial system are then frequently expressed linked to the eukaryotic protein. Fusion proteins are used for the analysis of structure, purification, function, and expression of heterologous gene products.

fusogen any agent, or set of conditions, that gives rise to fusion of membranes, including cell membranes (and hence of cells). Killed Sendai virus was formerly much used for this purpose but now polyethylene glycol is commonly used as a fusogen particularly in the preparation of hybridomas for the production of monoclonal antibodies. —**fusogenic** *adj.*

futile cycle any metabolic cycle that, if not controlled, acts as an ATPase and hence converts chemical energy (stored as ATP) to heat. For example, a coupling of phosphofructokinase, which converts fructose 6-phosphate to fructose 1,6-bisphosphate at the expense of ATP, with fructose-bisphosphatase, which hydrolyses fructose 1,6-bisphosphate to fructose 6-phosphate and (inorganic) phosphate, can form a cyclic process whose net effect is merely the hydrolysis of ATP to ADP and phosphate. A futile cycle may be an important control mechanism in some physiological conditions.

fuzzy coat *or* **fuzzy layer** the indistinct layer seen on electron microscopy outside the cell coat of various eukaryotic cells, e.g. cells of mammalian intestinal epithelium and a number of single-celled amoebae. It is composed principally of glycoproteins.

Fv fragment the N-terminal part of the **Fab fragment** of an immunoglobulin molecule, consisting of the variable portions of one light chain and one heavy chain.

FYN a gene family encoding nonreceptor tyrosine kinases of the Src family (*see* ***src***) that are implicated in the control of cell growth. The gene product, $p59^{fyn}$, associates with the p85 subunit of **1-phosphatidylinositol 3-kinase**. The proteins undergo myristoylation and phosphorylation on serine and tyrosine residues; overexpression transforms fibroblasts. Example, database code KFYN_HUMAN, 536 amino acids (60.56 kDa). The alternative gene symbols are *SYN* (from *src/yes*-related novel gene) and *SLK*.

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Gg

g *symbol for* **1** gram. **2** gaseous state. **3** gluon.

g **1** *symbol for* acceleration of free fall (formerly known as acceleration due to gravity). **2** *abbr. for gauche*.

g_n *symbol for* standard acceleration of free fall, a fundamental physical constant equal by definition to 9.806 65 m s^{-2}.

G *symbol for* **1** giga+ (SI prefix denoting 10^9 times). **2** gauss (alternative to Gs). **3** a residue of the α-amino acid glycine (alternative to Gly). **4** a residue of the base guanine in a nucleic-acid sequence. **5** a residue of the ribonucleoside guanosine (alternative to Guo). **6** a residue of the monosaccharide glucose (alternative to Glc). **7** ganglioside.

G *symbol for* **1** Gibbs energy. **2** gravitational constant. **3** weight (alternative to *W* or *P*). **4** electric conductance.

Ga *symbol for* gallium.

Ga_2 *symbol for* galabiose (alternative to $GaOse_2$).

Ga_3 *symbol for* galatriaose (alternative to $GaOse_3$).

GA *abbr. (sometimes) for* **1** glyceric acid. **2** glutamic acid. **3** glucuronic acid.

GAA a codon in mRNA for L-glutamic acid.

GABA *abbr. for* γ-amino-*n*-butyric acid or γ-aminobutyrate.

GABAergic **1** describing a nerve or other cell that is acted upon by γ-aminobutyrate. **2** describing nerves that act by releasing γ-aminobutyrate.

GABA-gated channel *see* **GABA receptor**.

GABA-modulin a brain protein that down-regulates the high-affinity binding site for γ-amino-*n*-butyric acid (GABA) on synaptic membranes.

GABA receptor any of several membrane proteins that bind γ-aminobutyrate (GABA) and mediate its effects as an inhibitory neurotransmitter. Two main types have been distinguished: $GABA_A$ receptors, known also as GABA-gated channels, which function as a Cl^- channel; and $GABA_B$ receptors, which are G-protein-coupled receptors. **Baclofen** is a potent GABA mimetic that is selective for the $GABA_B$ receptor; **muscimol** is its counterpart for the $GABA_A$ receptor. The $GABA_A$ receptor is multimeric, with α (types $\alpha1$–$\alpha6$), β (types $\beta1$–$\beta4$), γ (types $\gamma1$–$\gamma3$), δ, and ρ subunits. Examples (all precursors, human): α_1, database code GAA1_HUMAN, 456 amino acids (51.71 kDa); β_1, database code GAB1_HUMAN, 474 amino acids (54.18 kDa); γ_2, database code GAC2_HUMAN, 467 amino acids (54.12 kDa); ρ_1, database code GAR1_HUMAN, 473 amino acids (55.19 kDa). Subunits α and β have four putative transmembrane segments, with a domain distribution closely similar to that seen in the nicotinic acetylcholine receptor (nAChR) (*see* **cholinoceptor**), with some homology between specific regions of the two receptor types: for the α subunit with the M1 region of nAChR, and for the β subunit with regions M1–M3. Increased Cl^- ion flux brings about hyperpolarization of an excitatory neuron, which inhibits it from firing on receipt of a normal impulse. **Benzodiazepine** drugs interact with $GABA_A$ receptors; co-expression studies with cloned subunit variants have indicated that the γ subunit confers benzodiazepine sensitivity. The mode of action of $GABA_B$ receptors remains unknown. Indications variously suggest they may be coupled through G-proteins to stimulation of outward K^+ current, inhibition of inward Ca^{2+} channels, inhibition of adenylate cyclase, and stimulation of the phosphatidylinositol–Ca^{2+} system. *See also* **chloride channel**.

gabase *an informal name for* aminobutyrate aminotransferase (EC 2.6.1.19).

GABA shunt *abbr. for* γ-aminobutyrate shunt.

GABA transaminase *see* **4-aminobutyrate transaminase**.

GAC a codon in mRNA for L-aspartic acid.

G-actin the monomeric form of **actin**.

Gaddum equation a relationship, suggested to replace the **Hill–Langmuir equation**, that describes the situation when two ligands, A and B, are in equilibrium with a common binding site. It is:

$$P_{AR} = [A]/K_A(1 + [B]/K_B) + [A],$$

where P_{AR} is the proportion of the binding sites occupied by ligand A; the square brackets indicate concentrations. *Compare* **Schild equation**. [After (Sir) John Henry Gaddum (1900–67), British pharmacologist.]

gadelaidate *the trivial name for* (*E*)-eicos-9-enoate, CH_3–$[CH_2]_9$–CH=CH–$[CH_2]_7$–COO^- (*trans* isomer), the anion derived from gadelaidic acid, (*E*)-eicos-9-enoic acid. *Compare* **gadoleate**.

gadoleate *the trivial name for* (*Z*)-eicos-9-enoate, CH_3–$[CH_2]_9$–CH=CH–$[CH_2]_7$–COO^- (*cis* isomer), the anion derived from gadoleic acid, (*Z*)-eicos-9-enoic acid. *Compare* **gadelaidate**.

gag a gene that encodes the glucosaminoglycan core protein for a **retrovirus**. It is named from group-specific antigen gene, or glucosamino glycan gene. Example from avian erythroblastosis virus: database code AEVGAG, 962 amino acids (108.19 kDa). *See also* ***erbA***, ***erbB***.

GAG **1** a codon in mRNA for L-glutamic acid. **2** *abbr. for* glucosaminoglycan.

Gaia a theory of the role of biota in the maintenance of a climatic homeostasis, proposed by James Lovelock [(1919–), British biochemist] in 1979. The original concept, and still the heart of the philosophy, is that all of the living organisms that inhabit the Earth can be regarded as a single vast organism capable of manipulating the atmosphere, geosphere, and hydrosphere to suit its needs. Lovelock named this organism Gaia, after the Greek goddess of the earth.

Gal *symbol for* a residue (or sometimes a molecule) of the aldohexose galactose. In the condensed system of symbolism of sugar residues, it signifies specifically a galactose residue with the common configuration and ring size, i.e. D-galactopyranose.

GAL4 a gene involved in the regulation of galactose utilization in yeast. The GAL4 protein (database code GAL4_YEAST, 881 amino acids (99.39 kDa)) has a zinc-finger motif for binding to its upstream activator sequence (UAS), which it then activates, and a site for binding the complex of the GAL80 protein – encoded by the *GAL80* gene – and galactose. When this is bound, activation by GAL4 protein is prevented.

GalA *symbol for* a residue (or sometimes a molecule) of the uronic acid galacturonic acid.

galabiose *symbol*: Ga_2 *or* $GaOse_2$; *the trivial name for* the disaccharide Gal(α1-4)Gal.

galactan any glycan composed solely of galactose residues. The galactans thus form a subgroup of plant hemicelluloses.

galactitol *or* ***meso*-galactitol** *or (formerly)* **dulcitol** *the trivial name for* the hexitol formally derived by reduction of the aldehyde group of either D- or L-galactose. It is optically compensated internally and therefore does not require D or L as a configurational descriptor; the prefix *meso-* may however be added for clarity. It occurs widely especially in seaweeds and higher plants.

galacto- *prefix (in chemical nomenclature)* indicating a particular configuration of a set of (usually) four contiguous CHOH groups, as in the acyclic form of D- or L-galactose. *See* **monosaccharide**.

galactoceramide *see* **galactosylceramide**.

galactocerebroside *see* **galactosylceramide**.

galactokinase EC 2.7.1.6; *systematic name*: ATP:D-galactose 1-phosphotransferase. An enzyme that catalyses the phosphorylation by ATP of D-galactose to D-galactose 1-phosphate, with release of ADP; this is the first step in the metabolism of

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galactose. Example from *Escherichia coli*: database code GAL1_ECOLI, 381 amino acids (41.26 kDa).

galactolipid any **glycolipid** containing one or more residues of galactose and/or *N*-acetylgalactosamine. The term includes **galactosylceramide** and **galactosyldiacylglycerol**.

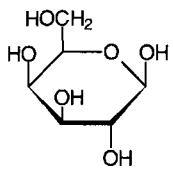
galactomannan any heteroglycan containing D-galactose and D-mannose residues; the structures have not been fully elucidated. They occur in seeds of various plants and trees, probably as storage polysaccharide. *See also* **guaran**.

galactoprotein A *abbr.*: Gap A; *an alternative name for* **fibronectin**.

galactosaemia *a variant spelling* (*esp. Brit*) *of* **galactosemia**.

galactosamine *symbol*: Gal*p*N; *the trivial name for* the aminodeoxysugar 2-amino-2-deoxygalactopyranose; there are two enantiomers, D- and L-galactosamine. D-Galactosamine (*symbol*: D-Gal*p*N), formerly known as **chondrosamine**, is a constituent (commonly as its *N*-acetyl derivative) of some glycolipids and of chondroitin sulfate, dermatan sulfate, and many bacterial glycosaminoglycans.

galactose *symbol*: Gal; *the trivial name for* the aldohexose *galacto*-hexose; there are two enantiomers, D- and L-galactose. D-Galactose (*symbol*: D-Gal), commonly known as galactose, and formerly known as **brain sugar** or **cerebrose**, rarely occurs free but is widely distributed in combined form in plants, animals, and microorganisms as a constituent of many oligo- and polysaccharides; it occurs also in **galactolipids** and as its glucoside in **lactose** and **melibiose**. Residues of both D-galactose and 3,6-anhydro-L-galactose (*symbol*: 3,6An-L-Gal) occur in the disaccharide **agarobiose** and in polysaccharides such as **agaropectin** and **agarose**.



β-D-galactose

galactose/glucose binding protein a signal transducing protein for bacterial chemotaxis. Example from *Escherichia coli*: database code NRL_2GBP, 309 amino acids (33.33 kDa); 3-D structure known.

galactosemia *or* (*esp. Brit.*) **galactosaemia** comparatively rare condition in humans in which there is a supranormal concentration of D-galactose in the blood and a specific inability to metabolize galactose. It is caused either by (1) a hereditary autosomal recessive trait in which there is a virtual absence of **UDPglucose–hexose-1-phosphate uridylyltransferase** activity; or less frequently (2) an inherited autosomal recessive trait in which there is a deficiency in **galactokinase** activity.

galactose oxidase EC 1.1.3.9; a copper-containing enzyme that catalyses the oxidation by dioxygen of D-galactose to D-*galacto*-hexodialdose and H_2O_2. Example from the fungus *Cladobotryum dendroides*: database code NRL_1GOG, 639 amino acids (68.44 kDa); 3-D structure known.

galactose-1-phosphate uridylyltransferase *see* **UDPglucose–hexose-1-phosphate uridylyltransferase**.

galactose-6-sulfate sulfatase *see* ***N*-acetylgalactosamine-6-sulfatase**.

galactosidase either of two types of enzyme: **α-galactosidase** EC 3.2.1.22; *systematic name*: α-D-galactoside galactohydrolase; *other name*: melibiase. An enzyme that hydrolytically removes terminal nonreducing α-D-galactose residues in α-galactosides, including galactose oligosaccharides, galactomannans, and galactolipids. Example from *Escherichia coli*: database code AGAL_ECOLI, 451 amino acids (50.60 kDa). **β-galactosidase** EC 3.2.1.23; *systematic name*: β-D-galactoside galactohydrolase; *other name*: lactase. An enzyme that removes terminal β-D-galactose residues in β-galactosides by hydrolysis. Example, *lacZ* gene product of *E. coli*: homotetramer, similar to other glycosyl hydrolases, database code BGAL_ECOLI, 1023 amino acids (116.22 kDa).

galactoside any **glycoside** in which the sugar moiety is galactose.

galactoside acetyltransferase EC 2.3.1.18; *recommended name*: galactoside *O*-acetyltransferase; *systematic name*: acetyl-CoA:β-D-galactoside 6-acetyltransferase; *other name*: thiogalactoside transacetylase. An enzyme that catalyses the acetylation by acetyl-CoA of β-D-galactoside to 6-acetyl-β-D-galactoside with release of GDP. Such an enzyme is the *lacA* gene product in *Escherichia coli* (*see* ***lac* operon**). Its function remains unclear. Example from *E. coli*: database code THGA_ECOLI, 203 amino acids (22.80 kDa).

galactoside 3(4)-L-fucosyltransferase EC 2.4.1.65; *systematic name*: GDP-L-fucose:β-D-galactosyl-*N*-acetyl-D-glucosaminyl-R 4-L-fucosyltransferase; *other name*: Lewis transferase. An enzyme that catalyses the transfer by GDP-L-fucose of fucose to 1,3-β-D-galactosyl-*N*-acetyl-D-glucosaminyl-R to form 1,3-β-D-galactosyl-(α-1,4-L-fucosyl)-*N*-acetyl-D-glucosaminyl-R with release of GDP; this forms the blood group determinant Le^a of **Lewis antigen**. The enzyme also acts on the corresponding 1,4-galactosyl derivative, forming 1,3-L-fucosyl links. It is a type II membrane glycoprotein, and a product of the Lewis blood group locus: database code GFT_HUMAN, 361 amino acids (42.07 kDa).

β-galactoside permease any of several transport proteins in bacteria that facilitate the uptake of β-galactosides. An example is melibiose carrier protein from *Klebsiella pneumoniae*: database code MELB_KLEPN, 471 amino acids (52.27 kDa). This is responsible for melibiose transport; it is capable of using hydrogen and lithium cations as coupling cations for co-transport, depending on the particular sugar transported (e.g. H^+-melibiose, Li^+-lactose), but cannot recognize Na^+ ions although it is an integral membrane protein of the sodium:galactoside symporter family. *See also* **lactose permease**.

galactosylceramidase EC 3.2.1.46; an enzyme that catalyses the hydrolysis of D-galactosyl-*N*-acylsphingosine to D-galactose and *N*-acylsphingosine. Example from human: database code JC2397, 669 amino acids (75.06 kDa).

galactosylceramide *the recommended term for* any D-galactosyl-*N*-acylsphingosine, i.e. any **cerebroside** in which the sugar moiety is D-galactose (less correctly termed **galactoceramide** or **galactocerebroside**).

galactosylceramide lipidosis *or* **Krabbe's disease** *or* **globoid cell leukodystrophy** one of a number of **sphingolipidoses** or sphingolipid lysosomal storage diseases. A rapidly progressive, invariably fatal, hereditary (autosomal recessive) disease of human infants caused by deficient activity of galactocerebroside β-galactosidase (galactosylceramidase; EC 3.2.1.46). Clinical symptoms usually start between the ages of 3 and 6 months and the condition is characterized by severe mental and motor deterioration and the presence of numerous globoid cells containing galactosylceramide in the white matter of the brain.

galactosylceramide sulfotransferase EC 2.8.2.11; an enzyme involved in **sulfatide** biosynthesis that catalyses the reaction between a galactosylceramide and 3′-phosphoadenylylsulfate to form galactosylceramide sulfate and adenosine 3′,5′-bisphosphate.

galactosyldiacylglycerol any of a class of lipids in which one or two galactose residues are in glycosidic linkage with a 1,2-diacylglycerol (loosely termed mono- and digalactosyldiacylglycerols), more specifically as, e.g., 1,2-diacyl-*sn*-glycerol 3-β-D-galactoside or (preferred, as glycosphingolipids are named this way) 1,2-diacyl-3-β-D-galactosyl-*sn*-glycerol. They are widely distributed in plants and are the main constituent lipids of chloroplasts, where they occur in the thylakoid membrane. They are also present in mitochondria.

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β-1,3-galactosyl-*O*-glycosyl-glycoprotein β-1,6-*N*-acetylglucosaminyltransferase EC 2.4.1.102; *other names*: *O*-glycosyl-oligosaccharide-glycoprotein; *N*-acetylglucosaminyltransferase I; β^6-*N*-acetylglucosaminyltransferase; core debranching enzyme; an enzyme that catalyses the reaction between UDP-*N*-acetyl-D-glucosamine and β-D-galactosyl-1,3-*N*-acetyl-D-galactosaminyl-R to form β-D-galactosyl-1,3-(*N*-acetyl-β-D-glucosaminyl-1,6)-*N*-acetyl-D-galactosaminyl-R with release of UDP. It introduces branches into O-linked glycoprotein oligosaccharides. Example from human: database code G6NT_HUMAN, 428 amino acids (49.73 kDa).

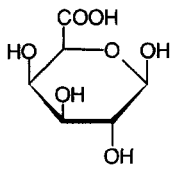
galactosyl transferase any enzyme belonging to the sub-subclass hexosyltransferases, EC 2.4.1, for which the glycosyl group is galactosyl; the acceptor is typically another carbohydrate molecule or lipid. *See also* **B-transferase**, **lactose synthase**, **Lewis transferase**.

galactowaldenase *a former name for* **UDPglucose 4-epimerase**.

galacturonan *or (formerly)* **polygalacturonide** any glycan composed solely of galacturonic-acid residues; a specific kind of glycuronan.

galacturonate **1** the anion of galacturonic acid. **2** any salt or ester of galacturonic acid.

galacturonic acid *symbol*: GalA *or (formerly)* GalU *or* GalUA; the uronic acid formally derived from galactose by oxidation of the hydroxymethylene group at C-6 to a carboxyl group. There are two enantiomers, D- and L-galacturonic acid; D-galacturonic acid is a component of plant gums and bacterial cell walls.



β-D-galacturonic acid

galanin a biologically active neuropeptide with a wide distribution in the central neurons of several mammalian species. Human galanin is the 30-residue sequence

GWTLNSAGYLLGPHAVGNHRSFSDKNGLTS;

porcine galanin had only 29 residues and differs at residues 16, 17 (I,D), 23 (H), 26 (Y), and 29 (A-NH_2). Galanin effects contraction of smooth muscle of the gastrointestinal and genitourinary tracts, and regulates somatotropin release; it may be involved in the control of adrenal secretion, and is also produced in the islets of Langerhans from stimulated intra-islet nerve terminals. It inhibits insulin release *in vivo* and *in vitro*, and inhibits formation of cyclic AMP in cells stimulated by **glucagon-related peptide**. A fragment, GWTLNSAGYLLGPHAI, is an agonist at the hippocampal galanin receptor. Example from pig (precursor): database code GALA_PIG, 123 amino acids (13.07 kDa); the hormone is derived from amino acids 33–61, with C-terminal amidation; a galanin message associated peptide (GMAP) is derived from amino acids 65–123.

galaptin any of various proteinaceous, β-galactoside-specific, animal lectins of relatively low molecular mass, that are isolated from a number of developing and adult tissues and are believed to mediate intercellular adhesion in some developmental systems.

galatriaose *symbol*: Ga_3 *or* $GaOse_3$; *the trivial name for* the trisaccharide Gal(α1-4)Gal(α1-4)Gal.

gall **1** an abnormal swelling or growth produced by a plant in response to the activities of various fungi, mites, and insects, especially members of the Cynipidae and Cecidomyidae. Insect eggs and larvae are often found in galls. **2** *a former name for* **bile**.

gallate **1** the anion of gallic acid, 3,4,5-trihydroxybenzoic acid, a phenolic acid. **2** any salt or ester of gallic acid. The esters and polyesters are very widely distributed in angiosperms, usually as **gallotannins**.

gall bladder a hollow, muscular organ, found in many vertebrates, that receives dilute **bile** from the liver, concentrates and stores it, and discharges it into the duodenum.

gallotannic acid *see* **tannic acid**.

gallotannin *or* **hydrolysable tannin** any **tannin** consisting of a molecule of a polyhydric alcohol (usually glucose) esterified with several gallic-acid molecules, each of which may itself be esterified with a further gallic acid molecule, and so on.

Gal*p* *symbol for* a galactopyranose residue.

Gal*p*A *symbol for* a residue (or sometimes a molecule) of galactopyranuronic acid.

Gal*p*N *symbol for* a residue (or sometimes a molecule) of the aminodeoxysugar **galactosamine**.

Gal*p*NAc *symbol for* a residue (or sometimes a molecule) of the acetamidodeoxysugar *N*-acetylgalactosamine.

GalU *or* **GalUA** *former symbol* for **galacturonic acid** (GalA now recommended).

galvanic cell *an alternative name for* **cell** (def. 3).

gamete a mature reproductive cell whose nucleus (and often cytoplasm) fuses with that of another gamete of similar origin but of opposite sex to form a **zygote**, which develops into a new individual. Gametes are haploid and are differentiated into male (+) and female (–).

gamma *symbol*: γ (lower case) *or* Γ (upper case); the third letter of the Greek alphabet. For uses *see* **Appendix A**.

gamma chain *or* **γ chain** **1** the **heavy chain** of an IgG immunoglobulin molecule. **2** one of the two types of polypeptide chain in a human fetal hemoglobin (Hb F) molecule.

gamma globulin *or* **γ-globulin** any of a band of serum proteins that migrate most slowly on electrophoresis. In humans this normally constitutes quantitatively the largest fraction of the total globulins. Since the γ-globulins are predominantly antibodies, and are not synthesized in the liver as are virtually all the other serum proteins, the albumin/globulin ratio has traditionally been a useful indicator of liver function. The γ-globulins may be separated from the other serum globulins in pooled adult serum and may then be used for administration by intramuscular injection to provide passive immunity in premature infants or for those in contact with cases of infectious hepatitis. Such γ-globulin preparations tend to form aggregates spontaneously and these can lead to severe anaphylactic reactions when administered intravenously on account of their ability to aggregate platelets and to activate complement and generate C3a and C5a anaphylatoxins. In certain diseases such as Bruton's congenital agammaglobulinemia the production of immunoglobulin in affected males is grossly depressed. In patients with myeloma the γ-globulin band on electrophoresis of serum proteins is markedly more prominent, indicating the presence of a raised antibody against an unknown antigen. *See also* **globulin**.

gamma helix *or* **γ helix** a configuration of a polypeptide chain in which each amide group forms hydrogen bonds with the groups five residues away in each direction along the chain. It has 5.1 amino-acid residues per turn; the translation along the helical axis is 0.99 Å per residue and 5.03 Å per turn.

gamma-peptidase *see* **X-Pro dipeptidase**.

gamma radiation *or* **γ-radiation** electromagnetic radiation with wavelengths in the range 0.1–100 pm (frequencies 3–3000 EHz) emitted by some atomic nuclei during ***transformation*** (def. 3). Gamma rays have shorter wavelengths than X-rays and higher photon energies.

gammopathy any pathological disturbance of gamma-globulin metabolism. Gammopathies may be monoclonal or polyclonal and are associated with increased immunoglobulin synthesis.

gamone any of a group of biological agents secreted by gametes that act on gametes of the opposite sex to initiate the progesses leading to fertilization. They may be subdivided into

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gynogamones, liberated from female gametes, and **androgamones**, liberated from male gametes.

ganciclovir 9-[(1,3-dihydroxy-2-propoxy)methyl]guanine; a nucleoside analogue of **acyclovir** that is more potent against cytomegalovirus. It is converted through ganciclovir mono- and diphosphate to ganciclovir triphosphate, which inhibits viral DNA synthesis by inhibition of viral DNA polymerase.

ganglion (*pl.* **ganglia**) a cluster of nerve cells and associated glial cells located outside the central nervous system.

ganglioside any ceramide oligosaccharide carrying, in addition to other sugar residues, one or more sialic residues. Gangliosides are so named because they were first isolated from ganglion cells (neurons) of the grey matter of the brain but are in fact widely distributed in vertebrate tissues. They are *N*-acetyl- (or *N*-glycoloyl-) neuraminosyl-(X)osylceramides, where (X) stands for the root name of the neutral oligosaccharide to which the sialosyl residue is attached; the acyl groups in the ceramide moiety are commonly stearoyl or lignoceroyl. Gangliosides are soluble in water and do not pass through semipermeable membranes, so may be purified by dialysis. In the Svennerholm system of abbreviations gangliosides are designated G for ganglioside, plus subscript M, D, or T for mono-, di-, or trisialo, respectively, the subscript letter being followed by a subscript arabic numeral to indicate the sequence of migration in thin-layer chromatograms. The principal gangliosides of human brain are:

(1) monosialo gangliosides: G_{M1}, Gal(β1-3)GalNAc(β1-4)(NeuAc(α2-3))Gal(β1-4)Glcβ1Cer (G_{A1} denotes the asialo derivative of G_{M1}); G_{M2}, GalNAc(β1-4)(NeuAc(α2-3))Gal(β1-4)Glcβ1Cer (G_{A2} denotes the asialo derivative of G_{M2}); G_{M3}, NeuAc(α2-3)Gal(β1-4)Glcβ1Cer;

(2) disialo gangliosides: G_{D1a}, NeuAc(α2-3)Gal(β1-3)GalNAc(β1-4)(NeuAc(α2-3))Gal(β1-4)Glcβ1Cer; G_{D1b}, Gal(β1-3)GalNAc(β1-4)(NeuAc(α2-8)NeuAc(α2-3))Gal(β1-4)Glcβ1Cer; G_{D3}, NeuAc(α2-8)NeuAc(α2-3)Gal(β1-4)Glcβ1Cer;

(3) trisialogangliosides: G_{T1a}, NeuAc(α2-8)NeuAc(α2-3)Gal(β1-3)GalNAc(β1-4)(NeuAc(α2-3))Gal(β1-4)Glcβ1Cer; G_{T1b}, NeuAc(α2-3)Gal(β1-3)GalNAc(β1-4)(NeuAc(α2-8)NeuAc(α2-3))Gal(β1-4)Glcβ1Cer.

ganglioside galactosyltransferase EC 2.4.1.62; *other name*: UDPgalactose–ceramide galactosyltransferase; an enzyme that catalyses the reaction between UDPgalactose and *N*-acetyl-D-galactosaminyl-(*N*-acetylneuraminyl)-D-galactosyl-D-glucosyl-*N*-acylsphingosine to form the **ganglioside** G_{M1}, with release of UDP.

gangliosidosis any of a group of inherited human diseases involving defects in **ganglioside** breakdown. They are characterized by: progressive mental and motor deterioration with fatal outcome; autosomal recessive inheritance; neuronal lipidosis secondary to storage of gangliosides and structurally related glycolipids, polysaccharides, or glycoproteins; and absence or severe deficiency of specific lysosomal glycohydrolases. The principal gangliosidoses are G_{M1} and G_{M2} gangliosidoses (the names indicating which ganglioside accumulates). G_{M1} gangliosidoses are due to a striking deficiency of β-galactosidase activity when tested using G_{M1} or galactose-containing glycoproteins as substrates. Type 1 or infantile G_{M1} gangliosidosis is a generalized gangliosidosis with bony involvement and onset of signs from birth or shortly after. Type 2 or juvenile G_{M1} gangliosidosis is of slower onset than type 1 and with milder bony abnormalities. There are three types of G_{M2} gangliosidosis. Type 1 G_{M2} gangliosidosis (*or* **Tay–Sachs disease**) is the commonest gangliosidosis, occurring especially in Ashkenazi Jews. It is caused by a severe deficiency of hexosaminidase A. Type 2 G_{M2} gangliosidosis (*or* **Sandhoff's disease**) occurs much less frequently than Tay–Sachs disease and is caused by severe deficiency of both hexosaminidases A and B; globoside accumulates in addition to G_{M2} in this disease. Type 3 or juvenile G_{M2} gangliosidosis is caused by either severe or partial deficiency of hexosaminidase A.

gangliotetraose *symbol*: Gg_4 *or* $GgOse_4$; *a trivial name for* the tetrasaccharide Gal(β1-3)GalNAc(β1-4)Gal(β1-4)Glc.

gangliotriaose *symbol*: Gg_3 *or* $GgOse_3$; *a trivial name for* the trisaccharide GalNAc(β1-4)Gal(β1-4)Glc.

$GaOse_2$ *symbol for* galabiose (alternative to Ga_2).

$GaOse_3$ *symbol for* galatriaose (alternative to Ga_3).

gap **1** a space introduced into the written form of a sequence of residues in a biopolymer to demonstrate homology with the sequence of a similar polymer from the same or another source. **2** a discontinuity in one of the two strands of duplex DNA resulting from enzymic elimination of one or more nucleotide residues. *Compare* **nick**.

GAP *abbr. for* **1** GnRH-associated peptide (*see* **gonadotropin-releasing hormone**). **2** *abbr. for* GTP-binding GTPase activating protein; a protein that activates the hydrolysis of GTP bound to certain monomeric proteins, especially $p21^{ras}$ (Ras, *see* **RAS**), but also for other Ras-related proteins, e.g. Rho (*see* **Rho protein**) and Ran (*see* **RAN**). Since GTP-bound Ras is the active form, binding to GAP inactivates it. The protein has SH2 and SH3 domains (*see* **SH domains**) and **pleckstrin homology domains**. The v-*ras* product is not stimulated by GAP. Example from *Bos taurus*: database code GTPA_BOVIN, 1044 amino acids (115.76 kDa).

Gap A *abbr. for* galactoprotein A (i.e. plasma **fibronectin**).

GAPDH *abbr. for* glyceraldehyde-3-phosphate dehydrogenase.

gap gene a type of gene in *Drosophila*. There are at least six gap genes, which act early in embryogenesis to make out the coarsest subdivisions of the embryo. Mutations in these genes result in gaps in the segmentation pattern; the **Krüppel** and **hunchback** proteins are products of gap genes.

gap junction *or* **nexus** any specialized area of the plasma membranes of apposed vertebrate cells where the membranes are 2–4 nm apart and penetrated by a **connexon** that bridges the extracellular space and provides open means of communication between the cytoplasm of one cell and that of the other cell. *Compare* **tight junction**.

gap phase either of the two phases, designated G_1 and G_2, in the cell-division cycle during **interphase** in growing eukaryotic cells during which there is no DNA synthesis.

gap repair the process of repair of a **gap** (def. 2) in one strand of a duplex DNA molecule.

garosamine 3-deoxy-4-*C*-methyl-3-(methylamino)-L-arabinose; a component of **gentamicins**.

gas a substance whose physical state is such that it always occupies the whole of the space in which it is contained, irrespective of the amount present. *See also* **gas laws**; **ideal gas**.

gas chromatography *abbr.*: GC; any form of chromatography in which the mobile phase is a gas. The term commonly refers to **gas–liquid (partition) chromatography** in which the stationary phase is a liquid, normally deposited on a solid support in a coiled column of glass or stainless steel, or the wall of a capillary column, but it also includes **gas–solid chromatography**, in which the stationary phase is a solid. The column is normally heated in an oven.

gas chromatography/mass spectrometry *abbr.*: GC/MS; an analytical technique that combines the separation process of **gas chromatography** with the highly selective detection technique of **mass spectrometry**.

gas constant *symbol*: R; a fundamental physicochemical constant; $R = 8.314\ 510\ (70)\ J\ K^{-1}\ mol^{-1}$.

gas exchange *(in physiology)* the exchange of gases between an organism and its environment. It includes oxygen uptake and carbon dioxide elimination in the respiration of all aerobic organisms, including plants, and carbon dioxide uptake and oxygen release in photosynthetic processes.

gas flow counter any gas-filled radiation detector in which the gas filling is renewed continuously. It may be operated in either the Geiger or the proportional regions of the voltage–current curve. Such devices are especially useful for detection and counting of alpha and soft-beta emitters, as no window is present to absorb the radiation.

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gas laws either of two laws describing the effects of changes in pressure, p, and thermodynamic temperature, T, on the volume, V, of an ideal gas. **Boyle's law** (*or* **Mariotte's law**) states that at constant temperature the volume of a given mass of gas is inversely proportional to the pressure; i.e. pV = a constant. **Charles's law** states that at constant pressure the volume of a given mass of gas is directly proportional to its thermodynamic temperature; i.e. V/T = a constant. These two laws may be combined in the expression: $pV \propto T$, or, for one mole of gas: $pV = RT$, where R is the **gas constant**.

gas–liquid (partition) chromatography an analytical method based on the partition chromatographic separation of the components of a mixture through the use of a stationary liquid phase held in place on a solid support and a mobile gas phase flowing over the liquid phase in a controlled manner. Typically, the column is heated to temperatures in the range 50–300 °C and the technique is applicable to compounds that partition appreciably into the vapour phase in that range. Detection of the eluents is commonly by a **flame ionization detector**.

gas–solid chromatography *see* **gas chromatography**.

gastr+ *a variant form of* **gastro+** (before a vowel).

gastric of, pertaining to, or derived from the stomach.

gastric acid the hydrochloric acid that is secreted from parietal (or oxyntic) cells of the wall of the stomach and forms part of the **gastric juice**.

gastric inhibitory peptide *abbr.*: GIP; *or* **glucose-dependent insulinotropic peptide** *or* **glucose-dependent insulin-releasing peptide** a 5 kDa polypeptide hormone produced by the K cells of the proximal small intestine and released into the bloodstream in response to the presence of glucose in the intestine. It is structurally related to glucagon, secretin, and vasoactive intestinal polypeptide having the sequence (human) YAEGTFISDYSIAMDKIHQQDFVNWLLAQKGKKNDWKHNITQ, porcine being similar but with Arg^{18} and Ser^{34}. The porcine hormone appears to be heterogeneous, the major component having 42 amino-acid residues and the main secondary component being two residues shorter at the N-terminus. Its two main physiological functions are the inhibition of gastric secretion and motility (**enterogastrone effect**), and the stimulation of insulin release when administered during hyperglycemia (**insulinotropic effect**); in the latter action GIP may be synonymous with **incretin**.

gastric juice the thin, clear, acidic fluid secreted by glands of the stomach mucosa in response to the ingestion of food. It contains mucus, intrinsic factor, hydrochloric acid (about 155 mM in humans) from the parietal cells, and **pepsinogen**, the precursor of pepsin proteolytic enzymes.

gastricsin EC 3.4.23.3; *other names*: pepsin C, pig parapepsin II; an enzyme of the pepsin family that appears to be present in the gastric juice of most vertebrates. It effects preferential cleavage at Tyr-|-Xaa bonds. It is a single-chain phosphoprotein formed by limited proteolysis of pepsinogen C with a more restricted specificity than pepsin A but high activity towards hemoglobin. Example, (precursor) from human: database code PEPC_HUMAN, 388 amino acids (42.38 kDa).

gastrin any of various members of a group of interrelated peptide hormones from the **G cells** of the pyloric antral mucosa of the stomach, and of the proximal duodenum, that strongly stimulate acid secretion by the stomach mucosa. There are three principal, biologically active forms: **big gastrin** (*or* G-34); **little gastrin**, (*or* G-17 *or* gastrin I); and **mini gastrin** (*or* G-14); these have 34, 17, and 14 amino-acid residues, respectively. The sequence of human big gastrin (gastrin I in parentheses, but with pE for the terminal Q) is pELGPQGPPHLVADPSKK(QGPWLEEEEEAYGWMDF-NH_2), where pE indicates pyroglutamyl. Each has a counterpart, e.g. G-17S (*or* gastrin II), in which the tyrosyl residue is sulfated. There are other, larger immunoreactive forms, known as **big-big gastrins**, that elute from a gel column before G-34. The entire physiological activity is possessed by the C-terminal tetrapeptide amide sequence that ends in a phenylalaninamide residue. The C-terminal pentapeptide sequence of gastrin is the same as that of **cholecystokinin** and **cerulein**. Example, gastrin precursor, a member of the gastrin/cholecystokinin family, a precursor for gastrin (17 amino acids) and big gastrin (34 amino acids) from human: database code GAST_HUMAN, 101 amino acids (11.38 kDa). *See also* **gastrinoma**, **pentagastrin**, **Zollinger–Ellison syndrome**.

gastrinoma a tumour of the gastrin-producing **G cells** of the pancreas, stomach, or duodenum. Gastrinomas are associated with high gastrin levels in the circulating blood, gastric hypersecretion, and fulminant gastroduodenojejunal ulcerations (**Zollinger–Ellison syndrome**).

gastrin receptor *see* **cholecystokinin receptor**.

gastrin-releasing protein a growth factor secreted by some small-cell lung cancers.

gastro+ *or (often before a vowel)* **gastr+** *comb. form* meaning stomach. [From Greek *gastēr*, belly.]

gastroenteric *an alternative term for* **gastrointestinal**.

gastrointestinal *or* **gastroenteric** of, or pertaining to, the stomach and intestines.

gastrointestinal hormone any member of a diverse group of peptides with hormone or hormone-like actions that occur in specific cells of the gastrointestinal tract, the pancreatic islets, and other locations. The best characterized include **cholecystokinin**, **gastric inhibitory polypeptide**, **gastrin**, **glucagon**, **insulin**, **motilin**, **neurotensin**, **pancreatic polypeptide**, **secretin**, **substance P**, and **vasoactive intestinal polypeptide**. *See also* **gut hormone**.

gastrula an early stage of development of an animal embryo, following the blastula, in which the cells are invaginating to form the rudiment of a gut cavity.

gas vacuole any membrane-bound, gas-containing, intracellular organelle. Gas vacuoles provide aquatic prokaryotes with buoyancy. *See also* **gas vesicle**.

gas vesicle the submicroscopic component of the gas vacuole in certain aquatic prokaryotes, especially cyanobacteria. It is constructed of molecules of a single protein (≈15 kDa), which form a monolayer enclosing a hollow space into which gases diffuse. Typically it is cylindrical with conical ends, 3–300 nm in diameter and 300–1000 nm in length.

GATA-1 *or* **ERYF1** *or* **GF-1** *or* **NF-E1** a transcriptional activator protein that serves as a general switch factor for erythroid development. It binds to DNA sites with the consensus sequence [A/T]GATA[A/G] within regulatory regions of globin genes and other genes expressed in erythroid cells. Other transcription factors with similar sequences are termed **GATA-type**. Example from human: database code GAT1_HUMAN, 413 amino acids (42.70 kDa).

GATase *see* **glutamine amidotransferase**.

gate *(in electronics)* **1** a logic circuit that gives an output signal only in response to a combination of two or more input signals. **2** a signal that allows or controls the passage of another signal.

gated channel a channel in the membrane of a cell (especially an excitable cell) that allows entry of ions into the cell only under specific conditions. *See also* **ligand-gated**, **voltage-gated ion channel**.

gating the opening and closing of a gated channel.

gating current an electric current arising from the movement of charged groups in the protein of the sodium-ion channels of excitable nerve membranes, during the passage of an action potential, prior to the opening of the channel.

g-atom *abbr. for* gram-atom or gram-atomic weight.

GAU a codon in mRNA for L-aspartic acid.

gauche *abbr.*: *g*; *(in chemical nomenclature)* a conformational descriptor indicating a synclinal conformation. *See* **conformation**.

Gaucher's disease an autosomal recessive inherited lysosomal storage disease showing several types, all of which involve some degree of **glucosylceramide** accumulation, especially in macrophages which are found in large numbers in spleen, bone marrow, and liver. The disease is due to a deficiency of

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glucosylceramidase (EC 3.2.1.45). There is a juvenile form which is associated with mental retardation, and a milder form that is not manifested until adult life. *See also* **saposin**. [After Philippe Charles Ernest Gaucher (1854–1918), French physician.]

gauss *symbol*: G *or* Gs; the cgs unit of magnetic flux; it is equal to a magnetic flux density of one maxwell per cm^2, one line of magnetic induction per cm^2, or 10^{-4} tesla.

Gaussian distribution *an alternative name for* **normal distribution**.

gavage the administration of food or other material in liquid form through a tube directly into the stomach; forced feeding in this manner.

Gb_3 *symbol for* globotriaose (alternative to $GbOse_3$).

Gb_4 *symbol for* globotetraose (alternative to $GbOse_4$).

G-banding *or* **Giemsa banding**; a commonly used procedure in which **Giemsa's stain** is used to identify chromosomal bands in a karyotype.

$GbOse_3$ *symbol for* globotriaose (alternative to Gb_3).

$GbOse_4$ *symbol for* globotetraose (alternative to Gb_4).

GBP *abbr. for* glucose bisphosphate (*formerly called* glucose diphosphate).

G-1,6-BP *abbr. for* glucose 1,6-bisphosphate (*formerly called* glucose 1,6-diphosphate).

Gc *symbol for* the glycoloyl group.

GC *abbr. for* gas chromatography.

GCA a codon in mRNA for L-alanine.

GC box a nucleotide sequence element common in eukaryotic promoters: consensus GGGCGC.

GCC a codon in mRNA for L-alanine.

G cell a gastrin-producing cell found in the antrum of the stomach and to a lesser extent in the mucosa of the duodenum, though the distribution varies in different species. In humans, G cells are small and pyriform while in dogs they are larger and triangular in shape. They can be identified by immunofluorescence using a gastrin-specific antibody.

GCG 1 a codon in mRNA for L-alanine. 2 a suite of computer programs widely used for nucleic acid and protein sequence analysis, structure prediction, and sequence alignment. It is available for **UNIX**, **VMS**, and **X Windows**, and is produced by **UWGCG**.

GC/MS *abbr. for* gas chromatography/mass spectrometry.

GCN4 a gene for a yeast transcription factor that binds, as a dimer, to the sequence TGA[C/G]TCA. The protein has a **leucine zipper**, and resembles ***FOS*** and ***JUN***. Database code: GCN4_YEAST, 281 amino acids (31.28 kDa).

G-CSF *abbr. for* granulocyte colony stimulating factor.

GCU a codon in mRNA for L-alanine.

Gd *symbol for* gadolinium.

GDC *abbr. for* Graves' disease carrier protein; it is similar in structure and some other properties to **ADP,ATP carrier protein**.

G4 DNA *abbr. for* DNA containing a **G-quartet**.

GDNF *abbr. for* glial cell line-derived neurotropic factor; a glycosylated disulfide-bonded homodimer that promotes survival and morphological differentiation of dopaminergic neurons. Human and rat GDNFs have 93% homology. The precursor, database code GDNF_HUMAN, 211 amino acids (23.72 kDa), yields a mature protein of 134 amino acids. *Compare* **brain-derived neurotropic factor**.

GDP *abbr. for* 1 guanosine diphosphate. 2 glucose diphosphate (now called glucose bisphosphate).

G-1,6-DP *abbr. for* glucose 1,6-diphosphate (now called glucose 1,6-bisphosphate).

GDP-fucosepyrophosphorylase *see* **fucose-1-phosphate guanylyltransferase**.

GDPM *or* **GDPmannose** *abbr. for* guanosinediphosphomannose.

GDPmannose 6-dehydrogenase EC 1.1.1.132; an enzyme that catalyses the reaction between GDP-D-mannose, 2 NAD^+ and H_2O to form GDP-D-mannuronate and 2 NADH. Example from *Pseudomonas aeruginosa*: ALGD_PSEAE, 436 amino acids (47.58 kDa).

GDPmannose 3,5-epimerase EC 5.1.3.18; an enzyme that catalyses the interconversion of GDP-D-mannose and GDP-L-galactose.

GDS *(in clinical chemistry) abbr. for* guanine deaminase.

Ge *symbol for* germanium.

Geiger counter *or* **Geiger–Müller counter** a device for detecting and measuring ionizing radiation (alpha or beta particles or gamma-ray photons). It consists of a glass envelope containing low-pressure gas and an anode and a cathode, between which a large electric-potential difference is maintained. The ions produced in the gas by the incoming ionizing radiation are accelerated towards their appropriate electrodes, causing a momentary drop in the potential between the latter. The voltage pulses so produced may be counted with a suitable electronic circuit. [After Hans Wilhelm Geiger (1882–1945), German physicist, and Erwin Wilhelm Müller (1911–77), German-born US physicist.]

Geiger region *or* **Geiger–Müller region** the part of the curve of applied voltage against number of ions collected for a given incoming radiation by a **Geiger counter**, where all possible ion-pairs, both primary and secondary, are collected; i.e. the signal is relatively independent of the applied voltage. *Compare* **proportional region**.

gel 1 a colloidal system, with the semblance of a solid, in which a solid is dispersed in a liquid. A gel has a finite, usually rather small, yield stress. 2 to become, or cause to become, a gel.

gelatin a heterogeneous mixture of water-soluble proteins of high average M_r derived from collagen by partial hydrolysis in either acid (type A) or alkali (type B). Collagen obtained by boiling skins, ligaments, tendons, etc. with water is also termed gelatin as also is collagen denatured by heating for 15 minutes at 45 °C, used as a substrate for **gelatinase**. It is colourless, or slightly yellow, and transparent, and occurs as brittle sheets, flakes, or coarse powder; these swell in water to form gels below 35–40 °C, containing 5–10 times as much water as gelatin by weight. Nutritionally gelatin is an incomplete protein containing only small amounts of certain essential amino acids, especially tryptophan. It is widely used in foods and in the manufacture of adhesives, photographic films and plates, and light filters.

gelatinase EC 3.4.24.24; *recommended name*: gelatinase A; *other names*: 72 kDa gelatinase; matrix metalloproteinase 2; type IV collagenase. An enzyme that catalyses the cleavage of **gelatin** and collagen types IV, V, VII, and X; it cleaves the collagen-like substrate sequence Pro-Gln-Gly-|-Ile-Ala-Gly-Gln; zinc and calcium are cofactors. It is a metallo (zinc) endopeptidase with **fibronectin** domains, and is produced by fibroblasts. Example from human (precursor): database code COG2_HUMAN, 660 amino acids (73.80 kDa); there is a large pre-pro region; the enzyme starts at amino acid 110.

gelation 1 the (usually reversible) act or process of forming a **gel** (def. 1) from a **sol**. *Compare* **solation**. 2 the solidification of a liquid by cold. —**gelate** *vb.*

gel chromatography *see* **liquid–gel chromatography**.

gel diffusion *(in immunology)* a technique in which antibodies and antigens are allowed to diffuse independently through a gel, often of agar, and form a precipitate within the gel where homologous antigens and antibodies meet in optimal proportions.

gel electrophoresis a type of **zone electrophoresis** in which the supporting medium is a gel of uniform concentration, commonly of polyacrylamide, agarose, or starch. *See* **polyacrylamide (gel) electrophoresis**. *Compare* **gradient (acrylamide) gel electrophoresis**.

gel filtration *or* **gel-filtration chromatography** *see* **gel-permeation chromatography**.

gel-filtration chromatography *see* **gel-permeation chromatography**.

gel-filtration high-performance liquid chromatography a technique of **gel-permeation chromatography** that uses a support material of high mechanical strength and chemical inertness

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thereby enabling separations to be effected under the conditions, and with the advantages of **high-pressure liquid chromatography**.

gel fluorography the application of **fluorography** (def. 2) to the detection of substances separated in gels, as by gel electrophoresis.

gellify to cause to become a **gel** (def. 1); to become gel-like; to **gel** (def. 2).

gelonin *or* **ribosome-inactivating protein** *or* **rRNA *N*-glycosidase** EC 3.2.2.22; *recommended name*: rRNA *N*-glycosidase; an extremely stable, potent toxin extracted from seeds of *Gelonium multiflorum* (a plant of the spurge family). It is a single-chain glycoprotein of 28–30 kDa containing terminal mannose residues. It acts as a powerful inhibitor of protein synthesis in cell-free systems but not in intact cells; it inactivates the 60S ribosomal subunit but has no effect on the 40S subunit. Its action is to hydrolyse one specific N-glycosidic bond of an adenosine on the 28S rRNA. In cell-free protein-synthesizing systems gelonin acts like the A chains of **abrin**, **ricin**, and **modeccin**, suggesting that it lacks the ability to bind to cell surfaces and enter cells. Example from *G. multiflorum*: RIPG_GELMU, 316 amino acids (35.42 kDa).

gel-permeation chromatography a method for the separation of substances in solution, *commonly known as* **gel filtration** *or* **gel-filtration chromatography**. The separation is based mainly on exclusion effects, such as differences in molecular size and/or shape or in charge, when the stationary phase is a swollen gel. The gel used is commonly a water-swollen insoluble carbohydrate polymer from which macromolecules are excluded and migrate without retention in the interstitial fluid. Substances of low or intermediate relative molecular mass penetrate into the gel particles to an extent that is, in most instances, determined by their molecular dimensions and the degree of cross-linking of the gel. The larger molecules therefore pass through the bed more rapidly than smaller molecules. The technique can be used to determine the relative molecular mass (M_r) of unknown materials, since, for a particular column, elution occurs at a volume determined by the equation

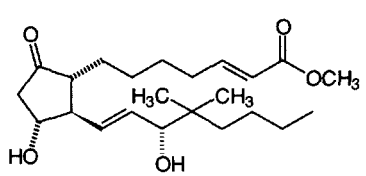
$$V_R/V_0 = 1 - \rho\log(M_r/M_{r0})$$

where V_R is the elution volume of the unknown, V_0 is the volume of the mobile phase in the column, M_r is the M_r of the unknown, M_{r0} is the M_r of the largest totally permeating molecule, and ρ is a factor that is a property of the column. Thus each column must be calibrated using standard proteins, and a plot made of the elution volumes against $\log M_r$ of the standards, from which the unknown M_r can be determined.

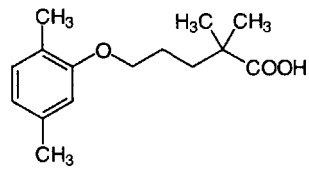
gelsolin a heat-labile, monomeric protein of apparent M_r 90 000 isolated from macrophages, platelets, and plasma. It appears to promote the gel–sol transformation of **actin** and may thereby be important in the control of locomotion, secretion, and endocytosis in these and other cells; β-actin has a similar action. There are two forms of gelsolin, plasma and cytoplasmic, generated by alternative splicing. The cytoplasmic, calcium-regulated, actin-modulating form binds to the barbed ends of actin monomers or filaments, preventing monomer exchange; it also promotes nucleation and binds with high affinity to fibronectin. Example (cytoplasmic form) from mouse: database code GELS_MOUSE, 731 amino acids (80.79 kDa).

gem- *prefix (in chemical nomenclature)* denoting the presence of **geminal** substituents.

gemeprost 16,16-dimethyl-*trans*-Δ^2-prostaglandin E_1 methyl ester; 11,15-dihydroxy-16,16-dimethyl-9-oxoprosta-2,13-dien-1-oic acid methyl ester; an analogue of **prostaglandin** E_1 with uterine stimulant activity.



gemfibrozil 2,2-dimethyl-5-(2,5-xylyloxy)valeric acid; an antihyperlipoproteinemic agent with actions similar to **clofibrate**.



geminal *(in chemistry)* describing two like groups or atoms attached to the same atom in a molecule, i.e. the geminal groups or atoms are separated by two bonds attached to the same atom. The presence of geminal substituents is denoted by the prefix *gem-* attached to the name of the compound. *Compare* **vicinal** (def. 2).

geminate occurring in pairs; doubled, twin.

+gen *or (after a consonant)* **+ogen** *comb. form* signifying producing or capable of producing (either directly or indirectly). In biological sciences it is used especially (1) with word-stems relating to physiological or pathological processes, states, conditions, etc., to denote a causative agent (e.g. antigen, lactogen, mutagen, estrogen); (2) with names of certain proteinases or blood components, to denote their inactive precursors or substances from which they can be derived by enzymic action (e.g. angiotensinogen, caseinogen, fibrinogen, trypsinogen) (*see also* **pro+** (def. 3), **zymogen**); (3) with names or name-roots of certain metabolites, to denote either a storage substance (e.g. glycogen, phosphagen) or a biosynthetic precursor (e.g. porphobilinogen); (4) with word-stems relating to physical properties (e.g. chromogen, luminogen). —**+genic** *or* **+genous** *adj. suffix.*

Genaminox KC *the proprietary name for* detergents similar to lauryldimethylamine oxide, but with different alkyl chain lengths (9–13).

Genapol *the proprietary name for* a series of nonionic polyoxyethylene detergents of the general formula $CH_3(CH_2)_x$–$O(CH_2CH_2O)_y$–H; Genapol X-080 has x = 12, y = 8, CMC 0.06–0.15 mM; Genapol X-100 has x = 12, y = 10, aggregation number 88, CMC 0.15 mM. *Compare* **C_xE_y**, **Lubrol**, **Triton**, **Tween**.

GenBank a large database of protein and nucleic-acid sequences. *See* **Appendix E**.

gene in classical genetics, a statistical entity that correlates with a particular phenotypic characteristic; the functional unit of heredity. Before their biochemical nature was understood, genes were defined in terms of units of mutation and/or recombination. Discovery of the role of DNA in genetic processes, followed by elaboration of the **central dogma** of protein synthesis, led to enunciation of the 'one gene–one enzyme' hypothesis, i.e. that a gene consisted of DNA that coded for a protein that performed the functions associated with the phenotypic expression of the gene. In current molecular genetics, the concept requires modification in a number of ways. First, the genomic DNA that codes for a polypeptide is associated with regulatory sequences such as promoters. Second, the polypeptide resulting from translation of mRNA may be subsequently split to give several polypeptides with different functions (*see* **polyprotein**). Third, the RNA transcribed may give rise to several different proteins as a result of **alternative splicing**. Three types of genes are now distinguished: those that are both transcribed into mRNA and translated into polypeptides (**structural genes**); those that are only transcribed into RNA (e.g. rRNA, tRNA); and those that function as regulators of the expression of the other two types (**regulator genes**). In diploid organisms a gene may occur in alternative forms

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(**alleles**). The term gene is sometimes used interchangeably with **cistron**.

gene amplification the selective, repeated replication of a certain gene or genes without a proportional increase in other genes in the genome. It occurs, e.g., in the DNA puffs of *Rhynchosciara* and some other flies and in the amplification of the genes coding for ribosomal RNA (so-called ribosomal DNA) in amphibian oocytes.

gene bank *an alternative name for* **gene library**.

gene cloning *see* **molecular cloning**.

gene cluster *or* **gene complex** any group of two or more functionally related genes that are closely linked on a chromosome. The genes of a gene cluster are often structural genes coding for the enzymes that catalyse the various steps of a metabolic pathway.

gene complex *an alternative name for* **gene cluster**.

gene dosage the number of times a particular gene is present in the genome.

gene duplication the phenomenon, occurring in some higher organisms, in which there is duplication of the DNA sequences representing particular genes. This process is thought to have played a decisive part in the evolution of these organisms, through the occurrence of different mutations in the two duplicated genes.

gene expression the process by which the information carried by a gene or genes becomes manifest as the phenotype. It involves **transcription** of the gene into complementary RNA sequences and, for structural genes, subsequent **translation** of mRNA into polypeptide chains and their assembly into the ultimate protein products. Gene expression is tightly regulated by **promoters, enhancers**, and **transcription factors**.

gene frequency a measure of the proportion of an allele in a given population, equal to the number of loci at which a given allele occurs, divided by the total number of loci at which it could occur.

gene library *or* **cloned library** *or* **gene bank** *or* **shotgun collection** a random collection of DNA fragments cloned in a **vector** (def. 3), and which may include all the genetic information of a particular species. It may be prepared from a variety of sources, including an extract of mRNA, in contrast to a **genomic library** which is prepared from genomic DNA.

gene mutation any **mutation** (def. 1) occurring within a single gene.

gene pool the sum of the genetic information in the reproductive members of a population of sexually reproducing organisms.

gene product any of the types of RNA (transcription products) or any of the proteins or protein subunits (translation products) synthesized biochemically on the basis of the information encoded in a genome.

general acid-catalysis **homogeneous catalysis** in which the catalysts are various hydron donors (acids). *Compare* **specific acid-catalysis**.

general base-catalysis **homogeneous catalysis** in which the catalysts are various hydron acceptors (bases). *Compare* **specific base-catalysis**.

generally labelled describing the labelling of a molecule in such a way that a radionuclide may be present at any or all (but not necessarily all) possible positions. *Compare* **uniformly labelled**.

general transcription factor any of the proteins whose assembly around the **TATA box** is required for the initiation of transcription of most eukaryotic genes.

generate *(in mathematics)* to conceive a point, line, or surface to be moving in a specified way so as to form a line, surface, or solid, respectively.

generation **1** the act or process of producing or reproducing, naturally or artificially. **2** the phase in a life cycle that extends from one to the immediately successive reproduction. **3** any group comprising all those members of a population who are equally removed from a common ancestor or from coeval ancestors.

generation of diversity *(in immunology)* the process by which a large number of variable regions are generated in the immunoglobulins. The **stem cell** genome contains multiple variants of L-chain V (variable) and J genes and of the H-chain V, J, and D (diversity) genes. As the stem cells differentiate, the maturing lymphocyte constructs particular L and H genes of virtually unique structure by a recombination process that randomly selects one out of each set of gene segments and assembles them, together with a C (for the constant region) gene into a mature H or L gene. This, combined with recombinational inaccuracies, somatic point mutations, and the varied combinations of L and H chains found in immunoglobulins results in a repertoire of millions of lymphocytes each with H and L genes encoding unique molecules. *See also* **immunoglobulin**.

generation time the time between division of a cell and that of its daughter cells, averaged over a whole cell population.

gene redundancy the presence in a cell of many copies of a single gene. The multiple copies may be inherited or result from selective **gene duplication** during development.

gene-regulatory protein any protein that binds to a specific DNA sequence to alter the expression of a gene.

+genesis *comb. form* denoting beginning or origin; development; generation. *See also* **+gen**. —**+genetic** *or* **+genic** *adj. comb. form.*

gene splicing biochemical and/or chemical manipulations with the object of attaching one DNA molecule to another. The neatest method is to cleave the DNA to be inserted (foreign DNA) with a **restriction endonuclease** that yields single-stranded ends that are complementary to each other. The **cloning vector** into which the foreign DNA is to be inserted is treated with the same endonuclease so that the complementary ends of the two DNAs specifically associate under annealing conditions and are subsequently covalently joined (spliced) through the action of **DNA ligase**. If the endonuclease produces fragments with 'blunt' or **flush ends** then a similar procedure is adopted. If the foreign DNA and the cloning vector have no common restriction sites then terminal **deoxynucleotidyl transferase** may be used which adds nucleotides to the 3′-terminal OH group of a DNA chain. For this purpose tails of poly(dT) and poly(dA) may be used. The transformed cells are then grown and those containing the spliced DNA are selected (cloning). The preferred method of splicing is one that allows the foreign DNA to be removed easily by means of a restriction endonuclease, preferably the same one that was initially used in splicing. By this means large amounts of the foreign DNA can be synthesized and used for many different purposes. Alternatively the cloned cells containing the foreign DNA can be used to permit the expression of a foreign protein which is then recovered.

genetic *or* **genetical** of or pertaining to **genetics**, **genes**, or the origin of something. —**genetically** *adv.*

genetically engineered describing a cell, strain, or organism whose phenotype has been altered by manipulation of its genetic material. *See* **genetic engineering**.

genetic block a reduction in the activity of a particular enzyme in a metabolic pathway as a result of gene mutation. A genetic block is termed **complete** when the particular enzyme activity is absent, or **incomplete** (*or* leaky) when the enzyme formed is defective and of limited activity.

genetic carrier *see* **carrier** (def. 9).

genetic code all the regularities in nucleotide sequence according to which genetic information for the sequences of all the polypeptides synthesized by transcription and translation is encoded in DNA (or RNA in some viruses). A sequence of three nucleotide residues (a codon) is required to code for one amino-acid residue, and since there are four different kinds of base in nucleic acids (apart from minor constituents), 4^3 i.e. 64 different nucleotide triplets can exist. But only 20 different amino-acid residues in polypeptides can be coded for; therefore the code is degenerate in that most amino acids can be

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specified by more than one codon. In terms of the sequence of nucleotides in mRNA, i.e. the nucleotides complementary to those in the genetic material, the genetic code, reading from the 5′ end to the 3′ end of each codon, is given in the table. (The letter A symbolizes a nucleotide residue containing *adenine*; G, *guanine*; C, *cytosine*; and U, *uracil*; each amino-acid residue is represented by its usual three-letter symbol.)

UUU: Phe	UCU: Ser	UAU: Tyr	UGU: Cys
UUC: Phe	UCC: Ser	UAC: Tyr	UGC: Cys
UUA: Leu	UCA: Ser	UAA: Ter†	UGA: Ter†
UUG: Leu	UCG: Ser	UAG: Ter†	UGG: Trp
CUU: Leu	CCU: Pro	CAU: His	CGU: Arg
CUC: Leu	CCC: Pro	CAC: His	CGC: Arg
CUA: Leu	CCA: Pro	CAA: Gln	CGA: Arg
CUG: Leu	CCG: Pro	CAG: Gln	CGG: Arg
AUU: Ile	ACU: Thr	AAU: Asn	AGU: Ser
AUC: Ile	ACC: Thr	AAC: Asn	AGC: Ser
AUA: Ile	ACA: Thr	AAA: Lys	AGA: Arg
AUG: Met‡	ACG: Thr	AAG: Lys	AGG: Arg
GUU: Val	GCU: Ala	GAU: Asp	GGU: Gly
GUC: Val	GCC: Ala	GAC: Asp	GGC: Gly
GUA: Val	GCA: Ala	GAA: Glu	GGA: Gly
GUG: Val	GCG: Ala	GAG: Glu	GGG: Gly

† termination codon. UAA was once called **ochre codon**; UAG, **amber codon**; UGA, **opal codon**.
‡ initiation codon. The methionine codon AUG is the most common starting point of translation of a genetic message but GUG sometimes serves.

The genetic code is almost universal but differences have been found in the DNA of mitochondria from a number of organisms. For example, in human mitochondria UGA codes for Trp and not for termination; AUA codes for Met and not for Ile; AGA and AGG are termination codons and do not code for Arg; AUA and possibly AUU act as initiation codons as well as AUG.

genetic colonization the introduction by a parasite of genetic information into a host such as to cause the host to synthesize products that only the parasite can use. This occurs in some plants, e.g., in cases of parasitism by *Agrobacterium* spp.

genetic complementation the phenomenon whereby the introduction of two chromosomes, each from different heterozygote cells and carrying different mutations in the same genetic region, results in the restoration of normal biochemical function, when this is deficient in either heterozygote.

genetic cross **1** any mating of two organisms that results in a **genetic recombinant**. **2** the offspring of two (or more) parent organisms produced by mating or other means.

genetic defect any alteration in the genetic information carried in an individual organism, the effect of which is to produce a phenotype that is at a disadvantage in competing with a normal organism of the same species or in meeting the challenges of its environment. *See also* **inborn error of metabolism**, **molecular disease**.

genetic disease any disease ultimately caused by a genetically determined biochemical defect. In the strict sense a genetic disease is only slightly influenced by environmental factors.

genetic drift **1** any change with time in gene frequency in a population. It may be either directed, **steady drift**, or undirected, **random drift**. **2** irregular, random fluctuations in gene frequency in a (relatively) small population caused by statistical effects.

genetic engineering the genetic manipulations used to produce individuals having a new combination of inherited properties. Such manipulation may be of two kinds: (1) cellular manipulation, involving the culturing of (haploid) cells and the hybridization of somatic cells (*see* **cell fusion**); and (2) molecular manipulation, involving the construction of artificial recombinant DNA molecules, their insertion into a **vector** (def. 3), and their establishment in a host cell or organism. The latter approach has been called **recombinant DNA technology**.

genetic information the information carried in a sequence of nucleotides in a molecule of DNA or RNA.

genetic locus *see* **locus**.

genetic map any diagram showing the linear order of, and the relative distances between, mutable sites on a chromosome as deduced from genetic recombination experiments.

genetic mapping any method that may be used to determine the positions of, and the relative distances between, genes of a linkage group or of sites within a gene (fine-scale mapping). In classical genetics, mapping relied on a study of recombination frequency and was measured in **morgans**. In molecular biology, mapping relies on the sequencing of DNA in a chromosome. Current work is aimed at mapping entire genomes. *See also* **genetic map**, **map unit**.

genetic marker **1** any genetically controlled phenotypic difference that can be used in analysing the genetic make-up of an organism. **2** any gene difference in either one or both alleles used in the detection of genetic recombination events.

genetic material the molecular carrier of primary genetic information that serves as a template for its own replication and provides the structural and regulatory information for the processes of protein synthesis and cell development. It consists of double-stranded DNA in higher organisms, bacteria, and most bacteriophages, single-stranded DNA in some bacteriophages, and RNA in the RNA viruses.

genetic polymorphism the regular and simultaneous existence in the same population of two or more discontinuous variants or genotypes, in frequencies that cannot be due to recurrent mutations, e.g. the different human blood groups.

genetic profiling *or* **DNA fingerprinting**, a technique for providing profiles of DNA fragments (resulting from digestion with restriction enzymes) that characterize a genome. The human genome is scattered with minisatellites, regions of DNA consisting of tandem repeats of short base sequence which can show extensive variation in the number of repeats, leading to multi-allelic variation and high degrees of heterozygosity. This extreme level of variation renders minisatellite or VNTR (**variable number tandem repeats**) loci invaluable as genetic markers. The DNA is digested with a suitable restriction endonuclease and the fragments are electrophoresed through agarose gel and transferred by blotting to a nylon filter. Hybridization is with a minisatellite probe labelled with ^{32}P. The use of the polymerase chain reaction (**PCR**) to amplify hypervariable loci, including very short tandem-repetitive microsatellites, has greatly increased the sensitivity of DNA typing systems and the ability to type degraded human DNA. The method can be used to identify an individual's DNA and also to trace the parentage of an individual. The method is not confined to humans but has been applied to a wide range of species.

genetic recombinant any organism produced by **genetic recombination**.

genetic recombination the processes by which a new genotype is formed by reassortment of genes resulting in gene combinations different from those that were present in the parents. In eukaryotes genetic recombination can occur by chromosome assortment, intrachromosomal recombination, or nonreciprocal interchromosomal recombination. Intrachromosomal recombination occurs by **crossing over**. In bacteria it may occur by genetic transformation, conjugation, transduction, or F-duction. *See also* **Holliday junction**.

genetics **1** the branch of biology concerned with heredity and variation in organisms. It embraces the phenomenology and physiology of heredity; the nature of genetic information; the storage of genetic material; the replication, mutation, transmission, and recombination of genetic material; and the way it

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is translated into systems that control development and metabolism, and determine the reappearance of parental characters among progeny. **2** the genetic features and constitution of any single organism, species, or group of organisms. *See also* **reverse genetics**.

genetic screening the testing of individuals or groups of individuals for some specific gene product or resulting metabolite for the purpose of identifying genetic defects or diseases.

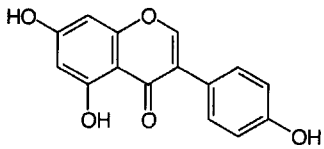
genetic transformation *see* **transformation** (def. 1).

genetic variance that part of the phenotypic variance caused by the varying genotypes of the individuals within a population.

genic of, or relating to, a gene or genes.

genin **1** *the class name for* the noncarbohydrate residue of steroid glycosides. It is used as a suffix in forming trivial names of the naturally occurring glycoside precursors; e.g. digitogenin (from digitonin), sapogenin (from saponin). **2** *a former name for* spirostan, 16,22:22,26-diepoxycholestane.

genistein 4,5,7-trihydroxyisoflavone; 5,7-dihydroxy-3-(4-hydroxyphenyl)-4*H*-1-benzopyran-4-one; an inhibitor of tyrosine-specific protein kinases and other protein kinases. It is a competitive inhibitor at the ATP binding site, which is a conserved structural feature in protein kinases.



genome the whole of the genetic information of an organism. It is contained as DNA in eukaryotes and prokaryotes, and as either DNA or RNA in viruses. A given organism has only one genome regardless of whether the organism is haploid, diploid, or polyploid. The term was originally used to denote one haploid set of chromosomes in a eukaryote organism. — **genomic** *adj.*

genome mutation any **mutation** (def. 1) occurring by alteration of the number of chromosomes in the genome.

genome-regulatory protein any site-specific protein involved in the regulation of transcription, such as a polymerase, repressor, or activator.

genomic blotting *an alternative name for* **Southern blotting**.

genomic DNA all of the DNA comprising one genome.

genomic library a set of clones containing DNA fragments that *in toto* embrace an entire genome. It is prepared by firstly randomly cutting the genomic DNA to give fragments of varying length. The average fragment length is controllable by discrimination in the choice of restriction enzymes used for cutting, and is selected to optimize the length such that fragments will contain entire open reading frames without excessive lengths of additional DNA at either end. Secondly the DNA fragments thus obtained are ligated into a suitable **vector** (def. 3), which is cloned in a host of choice.

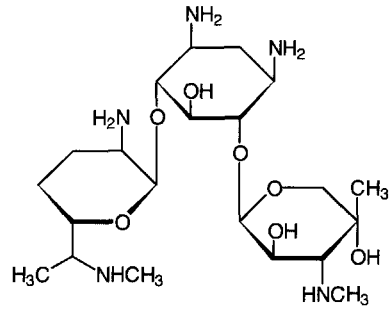
genophore the structural equivalent of a genetic **linkage group** in any organism. The term comprehends the linear chromosome of the (enveloped) eukaryon of all animal and plant cells, the circular chromosome of the (nonenveloped) prokaryon of cells of bacteria, the duplex DNA of mitochondria, chloroplasts, kinetoplasts, plasmids, and episomes, and the nucleic acid, whether DNA or RNA, single-stranded or double-stranded, of viruses.

genothèque a term proposed as an alternative to **gene library**. [From gene (ultimately from Greek *genos*, descent + *thēkē*, case, box.]

genotoxic exerting an effect by damaging or otherwise interfering with the action of a gene.

genotype **1** the total genetic constitution of an organism. It comprises the genetic information carried both in the chromosomes and extrachromosomally. *Compare* **phenotype**. —**genotypic** *adj.*

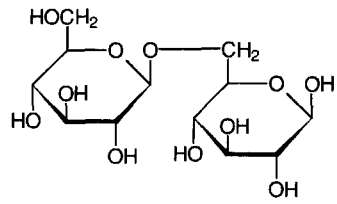
gentamicin *or* **gentamycin** any of a group of aminoglycoside antibiotics produced by fermentation of some *Micromonospora* spp. They are inhibitors of protein synthesis, and are particularly effective in the treatment of *Pseudomonas aeruginosa* infections.



gentamicin C_1

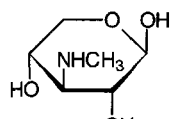
gentianose the trisaccharide, *O*-β-D-glucopyranosyl-(1→6)-*O*-α-D-glucopyranosyl-(1→2)-β-D-fructofuranoside. It is found in the rhizomes of many species of *Gentiana*.

gentiobiose *or (formerly)* **amygdalose** the disaccharide, *O*-β-D-glucopyranosyl-(1→6)-D-glucose. It is a component of some glycosides, e.g. **amygdalin**.



β-gentiobiose

gentosamine 3-deoxy-3-methylamino-D-xylose; a component of gentamicin A, one of the structural variants of **gentamicin**.



genus (*pl.* **genera**) *(in taxonomy)* a category used in biological classification consisting of species with a common phylogenetic origin that appear to be clearly differentiated from other species.

+geny *comb.form* denoting origin or mode of development. — **+genic** *adj.*

geometric isomer *or* **geometrical isomer** *an alternative term for* ***cis–trans*** **isomer**.

geometric isomerism *or* **geometrical isomerism** *an alternative term for* ***cis–trans*** **isomerism**.

geometric mean *or* **geometric average** for *n* positive numbers, the *n*th root of the product of the numbers. Thus for a set of positive numbers x_1, x_2, x_3, ... x_n, the geometric mean is $(x_1 \cdot x_2 \cdot x_3 \ldots x_n)^{1/n}$. *Compare* **mean**.

geotaxis the movement of an organism or a cell under the influence of a gravitational field. In **positive geotaxis** the organ-

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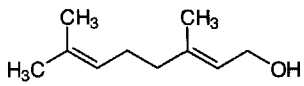
ism moves in the same direction as the gravitational field, while in **negative geotaxis** the movement is in a direction opposite to the gravitational field. —**geotactic** *adj.*

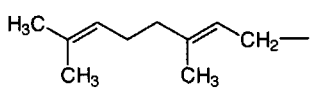
gephryin a cytoplasmic protein that associates with microtubules and is required for clustering of glycine receptors in spinal cord. It has a role in molybdoenzyme function in non-neural tissue. Example, GEPH_RAT, 736 amino acids (79.83kDa).

g-equiv *abbr. for* gram-equivalent or gram-equivalent weight.

geraniol (2*E*)-3,7-dimethyl-2,6-octadien-1-ol, a monoterpene alcohol with a sweet rose odour, present in oil of rose and other essential oils.

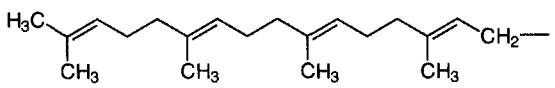


geranyl the (2*E*)-3,7-dimethyl-2,6-octadien-1-yl group. The 1-diphosphate derivative is an intermediate in the synthesis of cholesterol and in the formation of **geranylgeranyl** diphosphate.



geranyl-diphosphate synthase *see* **dimethylallyl*trans*transferase**.

geranylgeranyl the (2*E*,6*E*,10*E*)-3,7,11,15-tetramethyl-2,6,10,14-hexadecatetraen-1-yl group. The 1-diphosphate derivative is a substrate for enzymes introducing the geranylgeranyl group into proteins. *See also* **prenylation**.



geranylgeranyl pyrophosphate synthetase *see* **farnesyl-*trans*transferase**.

geranyl*trans*transferase EC 2.5.1.10; *systematic name*: geranyl-diphosphate:isopentenyl-diphosphate geranyl *trans*transferase; *other names*: farnesyl-diphosphate synthase; farnesyl pyrophosphate synthetase (*abbr.*: FPP synthetase). An enzyme of the pathway synthesizing **prenyl** groups, **sesquiterpenes**, and **cholesterol**. It catalyses the reaction between geranyl diphosphate and isopentenyl diphosphate to form *trans*,*trans*-farnesyl diphosphate with release of pyrophosphate. Example from yeast: database code FPPS_YEAST, 352 amino acids (40.48 kDa).

Gerbich system *abbr.*: Ge; a blood-group system whose antigenic determinants are located on the extracellular, glycosylated domain of **glycophorins** C and D (GPC and GPD). The polypeptide sequences of these give rise to several Ge phenotypes: on GPD the antigenic site for Ge2 resides between residues 1 and 17, and that for Ge3 resides between residues 19 and 34; on GPC, the antigenic site for Ge4 is at the N terminus, and that for Ge3 between residues 40 and 55.

GERL *abbr. for* Golgi, endoplasmic reticulum, lysosomes; a term formerly used to describe a specialized region of smooth **endoplasmic reticulum** with high levels of acid phosphatase and other acid hydrolase activities. It is thought to be a region where acid hydrolases are concentrated and packaged into lysosomes. It may also be concerned in packaging other materials, including epinephrine granules in the adrenal medulla, tyrosinase and other materials in premelanosomes in mouse melanomas, peroxidase, etc. in secretory granules in cells of parotid and submaxillary glands, and un-iodinated thyroglobulin in thyroid epithelial cells.

germ cell any cell of the **germ line**, including **gametes**.

germ-free describing any group of animals or plants that is bred and maintained in such conditions that they contain no microorganisms, either normal symbionts or abnormal, infective ones. *Compare* **gnotobiotic**.

germin a pepsin-resistant water-soluble glycoprotein of the walls of germinated plant embryos that may alter the properties of cell walls during germinative growth. Its synthesis coincides with the onset of growth in germination. The protein has oxalate oxidase activity. Example from *Triticum aestivum*: germin GF-2.8 precursor, homopentamer; database code GER2_WHEAT, 224 amino acids (23.58 kDa).

germ line any line of cells that gives rise to gametes and is continuous through the generations.

Gerstmann–Straussler syndrome a transmissible **spongiform encephalopathy** of humans, usually familial, characterized by widespread degeneration of the nervous system. *See also* **prion**. [After Joseph Gerstmann (1887–1969), Austrian neurologist.]

GF-1 *see* **GATA-1**.

GFR *abbr. for* (renal) glomerular filtration rate.

Gg_3 *symbol for* gangliotriaose (alternative to $GgOse_3$).

Gg_4 *symbol for* gangliotetraose (alternative to $GgOse_4$).

GGA a codon in mRNA for a glycine residue.

GGC a codon in mRNA for a glycine residue.

GGG a codon in mRNA for a glycine residue.

$GgOse_3$ *symbol for* gangliotriaose (alternative to Gg_3).

$GgOse_4$ *symbol for* gangliotetraose (alternative to Gg_4).

GGU a codon in mRNA for a glycine residue.

GH *abbr. for* growth hormone (i.e. **somatotropin**).

ghilanten *see* **antistasin**.

ghost an empty red-blood-cell membrane, usually obtained by lysis of red cells by the controlled reduction in the osmotic pressure of the suspending medium followed by restoration of normal osmotic conditions causing the membranes to reseal. Ghosts are extensively used in studies of the properties of membranes.

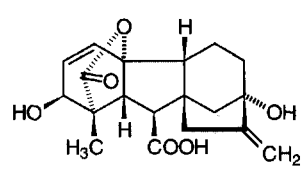
GHRF *abbr. for* growth hormone releasing factor (*see* **GHRH**).

GHRH *abbr. for* growth hormone releasing hormone; *other names*: growth hormone releasing factor (*abbr.*: GHRF) *or* somatoliberin; any of a family of peptide hormones that act on the anterior pituitary to stimulate the secretion of growth hormone and exert a trophic effect on the gland. Example from *Bos taurus*: database code SLIB_BOVIN, 44 amino acids (5.109 kDa). It is synthesized as a precursor; example from *Oncorhynchus nerka*: database code PACA_ONCNE, 173 amino acids (19.7 kDa). *See also* **GHRH receptor**.

GHRH receptor *abbr. for* growth hormone releasing hormone receptor; *other name*: growth hormone releasing factor receptor (*abbr.*: GRFR); any of a family of integral membrane proteins that bind GHRH and mediate its intracellular effects. These receptors are seven-transmembrane-helix receptors coupled to a G-protein that stimulates adenylate cyclase. A defect in this receptor ($Asp^{60} \rightarrow Gly^{60}$) is associated with hypoplasia of the anterior pituitary in mice. Example (precursor) from *Mus musculus*: database code GRFR_MOUSE, 423 amino acids (47.04 kDa).

GH-RIH *abbr. for* growth hormone release inhibiting factor (i.e. **somatostatin**).

gibberellin any of a widely distributed, multimembered group



gibberellic acid

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of highly modified C_{20} (and C_{19}) terpene plant hormones, the first of which was isolated from plants infected with the fungus *Gibberella fujikuroi*. The most important is gibberellin A_3, also known as **gibberellic acid**. Gibberellins accelerate shoot growth, and can actively stimulate RNA synthesis in dwarf mutant plants, making them grow like normal plants. Other physiological effects, e.g. overcoming the need for vernalization in long-day plants, have also been recorded.

Gibbs–Duhem equation an equation relating the chemical potential and concentration of a chemical species in a mixture at constant temperature and pressure. If n_i moles of species i, having chemical potential μ_i, are present in a mixture, then

$$\sum_i n_i d\mu_i = \sum_i x_i d\mu_i = 0$$

where $x_i = n_i/\sum_i n_i$ is the mole fraction and $d\mu_i$ is the change in chemical potential for dn_i, a small change in the amount of species i present, in moles. [After Josiah Willard Gibbs (1839–1903), US physical chemist, and Pierre Duhem (1861–1916), French physical chemist.]

Gibbs energy *or* **Gibbs free energy** *or* **Gibbs function** *symbol*: G; a thermodynamic property of a system; it is defined as $H - TS$, where H is the enthalpy, S the entropy, and T the temperature. For a molecule in solution, Gibbs energy is concentration-dependent. The Gibbs free energy (G_i) of the ith component is equal to the standard free energy of the component (G°_i, the free energy at unit activity) plus a term to adjust for concentration. Thus

$$G_i = G^\circ_i + RT\ln a_i,$$

where R is the gas constant, and a_i the activity of the ith component. The molar free energy is referred to as the **chemical potential**. *See also* **Gibbs free energy change**.

Gibbs energy diagram *or* **Gibbs energy profile** for a chemical reaction, a diagram showing the relative standard Gibbs energies of reactants, transition states, reaction intermediates, and products in the same sequence as they occur in the reaction.

Gibbs energy of activation *or* **Gibbs free energy of activation** *symbol*: $\Delta^\ddagger G^\circ$; the standard Gibbs energy difference between the transition state of a chemical reaction (either elementary or stepwise) and reactants.

Gibbs free energy change the difference in Gibbs free energy (G) at any instant in time between the reactants and products of any reaction. Thus for a reaction A + B ⇌ C + D, at any particular concentration of reactants and products, the free energy change, ΔG, for that state is calculated as

$$G_C + G_D - G_A - G_B.$$

Since, for each substance,

$$G_X = G_X^\circ + RT\ln a_x$$

(*see* **Gibbs energy**), this leads to

$$\Delta G = \Delta G^\circ + RT\ln\{a_C a_D/a_A a_B\};$$

$$\Delta G^\circ = \Delta G^\circ_C + \Delta G^\circ_D - \Delta G^\circ_A - \Delta G^\circ_B,$$

and is the **standard free energy change**. All chemical reactions proceed in the direction of negative free energy change until equilibrium is reached, at which point ΔG is zero. Since at equilibrium $a_C a_D/a_A a_B$ is the equilibrium constant K, it follows that the standard free energy change $\Delta G^\circ = -RT\ln K^\circ$ where K° is the standard equilibrium constant.

Gibbs–Helmholtz equation an equation that may be expressed as

$$\Delta G - \Delta H = T[\delta\Delta G/\delta T]_P$$

where ΔG is the change in Gibbs energy during a reaction, ΔH the increase in enthalpy, P the pressure, and T the temperature.

Giemsa's stain a stain used for staining chromosomes, in which it reveals bands known as **G-bands** (from the name). These are rich in A–T nucleotide pairs. Other compounds, e.g. the antibiotic olivomycin, stain G–C-rich bands known as **R-bands** (because they give the 'reverse' of the G-bands). [After Gustav Giemsa (1867–1948), German parasitologist.]

GIF *abbr. for* growth hormone-inhibitory factor (i.e. **somatostatin**).

giga+ *symbol*: G; **1** the SI prefix denoting 10^9 times. **2** (*in computing*) *prefix* used to indicate a multiple of 2^{30}, e.g. gigabyte.

gigantism a condition arising from the excessive release of **somatotropin** leading to an individual of excessive size. *Compare* **acromegaly**.

Gilbert, Walter (1932–), US theoretical physicist and molecular biologist; Nobel Laureate in Chemistry (1980) jointly with F. Sanger 'for their contributions concerning the determination of base sequences in nucleic acids' [prize shared with P. Berg].

Gilman, Alfred Goodman (1941–), US pharmacologist; Nobel Laureate in Physiology or Medicine (1994) jointly with M. Rodbell 'for their discovery of G-proteins and the role of these proteins in signal transduction in cells'.

GIP *abbr. for* gastric inhibitory peptide.

GIPL *abbr. for* glycoinositolphospholipid (*see* **GPI anchor**).

GIP receptor any of the integral membrane proteins that bind **gastric inhibitory peptide** (GIP) and mediate its intracellular effects. They are G-protein-coupled, seven-transmembrane-helix receptors that activate adenylate cyclase. Example (precursor) from *Rattus norvegicus*: database code GIPR_RAT, 455 amino acids (52.26 kDa); residues 1–18 are the signal peptide, 19–455 the receptor.

Gla *symbol for* a residue of the α-amino acid L-4-carboxyglutamic acid.

Glanzmann thrombasthenia *see* **von Willebrand factor**.

glass electrode an electrode made of glass whose potential, when immersed in a solution, is a function of the hydrogen-ion activity, i.e. pH, of the solution. A common form of glass electrode consists of a thin glass bulb inside which is mounted a reference electrode, often a silver/silver chloride electrode, immersed in a solution of constant pH and containing the ion to which the inner reference electrode is reversible. A number of special glasses have been made in an effort to extend the range of pH over which the electrode responds linearly, to reduce errors caused by other ions in solution, to extend its useful temperature range, etc.

Glc *symbol for* a residue (or sometimes a molecule) of the aldohexose **glucose**. In the condensed system of symbolism of sugar residues, Glc signifies specifically a glucose residue with the common configuration and ring size, i.e. D-glucopyranose. (*Note*: Glu is the symbol for a glutamic residue.)

GLC *or* **glc** *abbr. for* gas–liquid chromatography.

GlcA **1** *symbol for* a residue (or sometimes a molecule) of the uronic acid glucuronic acid. **2** *former symbol for* a residue (or sometimes a molecule) of the aldonic acid **gluconic acid** (no symbol now recommended).

Glc*f* *symbol for* a glucofuranose residue.

GlcN *symbol for* a residue (or sometimes a molecule) of the aminodeoxysugar **glucosamine**.

GlcNAc *symbol for* a residue (or sometimes a molecule) of the *N*-acetylated aminodeoxysugar ***N*-acetylglucosamine**.

Glc*p* *symbol for* a glucopyranose residue.

GlcU *or* **GlcUA** *former symbol for* glucuronic acid (GlcA now recommended).

GLI *abbr. for* glucagon-like immunoreactant (or glucagon-like immunoreactivity).

glia *or* **neuroglia** the special connective tissue of the central nervous system constituting some 40% of the total volume of the brain and spinal cord. It has supportive and nutritive functions and is made up of **glial cells** – oligodendrocytes, astrocytes, ependymal cells, and microglial cells.

gliadin *or (formerly)* **gliadine** any of a group of proline-rich proteins (**prolamins**) found in the seeds of the cereals wheat and rye. All gliadins are mixtures of simple proteins of similar composition and properties. They are differentiated from **glutenin**, with which they are associated in gluten, by their solubility in 70% aqueous ethanol. With water, gliadins form a sticky mass, which binds flour into a dough. They constitute

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the major seed storage proteins in wheat. Gliadins fall into two groups: α/β gliadins (*also* prolamin *or* gliadin AI–V) are in five homology classes; there are more than 100 copies of the gene per haploid genome; γ-gliadins are in three homology classes (classes BI–III). For both groups, sequence divergence between the respective classes is due to single base substitutions and to duplications or deletions within or near direct repeats. These proteins have nine motifs. Examples (precursors): α/β, database code GDA1_WHEAT, 262 amino acids (30.37 kDa); γ, database code GDB1_WHEAT, 304 amino acids (34.21 kDa). [French *gliadine*; from Greek *glia*, glue.]

glial cells *see* **glia**.

glial derived nexin a glycoprotein serine protease inhibitor, similar to **serpin**, that promotes neurite extension. Example (precursor) from human: database code GDN_HUMAN, 398 amino acids (43.95 kDa). *See also* **nexin**.

glial fibrillary acidic protein *abbr.*: GFAP; a class III **intermediate filament** and a cell-specific marker that, during the development of the central nervous system, distinguishes astrocytes from other glial cells. It is similar to other intermediate filament proteins. Example from human astrocyte: database code GFAP_HUMAN, 432 amino acids (49.82 kDa).

glibenclamide *see* **glyburide**.

glicentin a peptide of originally obtained as a component of porcine enteroglucagon and known at first as **porcine gut GLI-I**. It reacts fully with antisera to the N-terminal moiety of glucagon from pancreas. The known amino-acid sequence includes the entire sequences of **glicentin-related pancreatic peptide** (at residues 1–30) and pancreatic **glucagon** (at residues 33–61), and is identical with the N-terminal moiety of the sequence of proglucagon. It was initially thought to be composed of 100 amino-acid residues, hence the name.

glicentin-related pancreatic peptide *or* **glicentin-related pancreatic polypeptide** *abbr.*: GRPP; originally, any polypeptide material present in extracts of porcine pancreas and in the secretory granules of the pancreatic A cell that reacted with certain antisera to glicentin but not with any antisera to glucagon. The term is now usually applied to a specific component of such material that is a 30-residue peptide identical in sequence to the N-terminal 30-residue sequence of **proglucagon**, is secreted by the pancreas concomitantly with glucagon, and thus is probably a cleavage product of proglucagon.

GLI-I *see* **glicentin**.

gliostatin *see* **platelet-derived endothelial cell growth factor**.

GLIP *abbr. for* glucagon-like insulinotropic peptide; a gastrointestinal peptide that potentiates release of insulin. It is released during a meal and after oral glucose administration. It is GLP-1^{7-37}. *See* **glucagon**.

Gln *symbol for* a residue of the α-amino acid L-**glutamine** (alternative to Q or Z).

globin the colourless and basic protein moiety (and biosynthetic precursor) of **hemoglobin** and **myoglobins**. In normal human adult hemoglobin, the globin component comprises two nonidentical pairs of polypeptide chains, whereas in myoglobin there is only one polypeptide chain. Pharmaceutical globin is prepared by adding ox hemoglobin to acetone–HCl; this causes the heme groups to separate and remain in solution while the globin precipitates. It is used in the preparation of globin–insulin, which is absorbed more slowly than soluble insulin and has a prolonged action.

globo+ *prefix* for an oligosaccharide, signifying the core structure GalNAc(β1-3)Gal(α1-4)Gal(β1-4)Glc (I), present in **globoside** from which the term originated. Also, by derivation it signifies Gal(α1-4)Gal(β1-4)Glc, residues 2–4 of I. *Compare* **isoglobo+**.

globoside *or* **cytolipin K** *symbol*: $GbOse_4Cer$ *or* Gb_4Cer; globotetraosylceramide; ceramide globotetraoside; the major neutral glycosphingolipid in normal kidney and erythrocytes. The name originated from the discovery of this lipid on red cells, and led to the use of **globo+** as a root signifying this core carbohydrate structure. *Compare* **globotriaosylceramide**. *See also* **globotetrasylceramide**, **P system**.

globotetraose *symbol*: $GbOse_4$ *or* Gb_4; the tetrasaccharide GalNAc(β1-3)Gal(α1-4)Gal(β1-4)Glc. *See also* **P system**, **globo+**.

globotetraosylceramide *symbol*: $GbOse_4Cer$ *or* Gb_4Cer; a glycolipid having the structure

GalNAc(β1-3)Gal(α1-4)Gal(β1-4)GlcCer.

It is the P determinant in the **P system** of blood groups. *See also* **globo+**.

globotriaose *symbol*: $GbOse_3$ *or* Gb_3; the trisaccharide Gal(α1-4)Gal(β1-4)Glc. *See also* **globo+**.

globotriaosylceramide *symbol*: $GbOse_3Cer$ *or* Gb_3Cer; a glycolipid **globoside** having the structure Gal(α1-4)Gal(β1-4)GlcCer. It is the major neutral glycosphingolipid in leukocytes, platelets, liver, spleen, and most other non-neural tissues. It is the P^k determinant in the **P system** of blood groups. *See also* **globo+**.

globular protein any protein whose polypeptide chain(s) are folded so as to give the whole molecule a rounded shape.

globulin any simple, globular protein that is insoluble or sparingly soluble in water but soluble in dilute salt solutions, and can be precipitated from solution by half-saturating the solution with neutral ammonium sulfate. Globulins may be distinguished by, e.g., electrophoresis into α-, β-, and γ-globulins, or by ultracentrifugation into 7S globulins, 19S globulins, etc. *See also* **gamma globulin**, **immunoglobulin**.

glomerular filtrate the filtrate, free of cells and major plasma proteins, that passes from the blood through a renal glomerulus into the lumen of a nephron in the kidney.

glomerular filtration rate *abbr.*: GFR; the rate at which the **glomerular filtrate** is produced in the kidney(s). It is a measure of renal efficiency and is usually expressed in terms of the renal clearance of some substance, e.g. inulin, that is freely filterable by the glomerulus and is neither reabsorbed nor excreted by the renal tubules.

glomerulus (*pl.* **glomeruli**) **1** a knot of blood capillaries projecting into the capsular end of a nephron and from which the **glomerular filtrate** is formed. *See also* **Malpighian body**. **2** any compact tuft or tangled mass of processes, nerve fibres, or blood vessels. —**glomerular** *adj.*

glp a **regulon** of *Escherichia coli* encoding proteins required for the utilization of glycerol 3-phosphate and its precursors. Operons for enzymes of these pathways are controlled negatively by *glp* repressor and positively by the cyclic AMP–cyclic AMP receptor protein complex.

Glp *symbol for* a residue of the α-imino acid L-5-oxoproline (often known as pyroglutamic acid or pyrrolidinecarboxylic acid).

GLP *abbr. for* glucagon-like peptide (*see* **glucagon-related polypeptide**).

Glu *symbol for* a residue of the α-amino acid L-**glutamic acid** (alternative to E). (*Note*: Glc is the symbol for a glucose residue.)

gluc+ *a variant* (*sometimes, before a vowel*) *of* **gluco+**.

glucaemia *a variant spelling (esp. UK) of* glucemia; *see* **glycemia**.

glucagon a 3.5 kDa, single-chain, 29 residue hormone synthesized in the A cells of pancreatic islets and mammalian (except human) gastric mucosa. Formerly sometimes known as hyperglycemic-glycogenolytic factor (*abbr.*: HGF), or hyperglycemic factor. The amino-acid sequence is highly conserved, being identical in human and all other mammalian glucagons studied so far (except guinea-pig):

HSQGTFTSDYSKYLDSRRAQDFVQWLMNT;

there are two motifs, characteristic of the glucagon family. It is secreted in response to falling blood glucose levels and has an opposing action to that of **insulin** by increasing the glucose concentration in the blood. The effects of glucagon are mediated in responsive tissues by either (1) stimulation of adenyl-

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ate cyclase or (2) activation of inositolphospholipid-specific phospholipase C with increase in intracellular Ca^{2+} concentration. Its effects include the stimulation of glycogenolysis and gluconeogenesis in liver, increased lipolysis in adipose tissue, and increased insulin secretion. Three peptides (glucagon itself and glucagon-like peptides 1 and 2 (GLP-1 and -2)) derive from the precursor. These peptides have ≈50% similarity in their primary structure. The sequence for GLP-1 is the same in all mammalian species studied but its biological role is unknown. While GLP-1 is the major form in the pancreas, a smaller fragment, GLP-1^{7-36}-amide, predominates in the intestine. This is a potent stimulator of insulin secretion and is a potent inhibitor of gastric secretion. Receptors for this peptide have been shown to be present in rat insulinoma cell lines and in brain. Exendin$^{9-39}$ is a GLP-1 receptor antagonist. Intracerebroventricularly administered GLP-1 powerfully inhibits feeding in the starving rat. This effect is blocked by exendin$^{9-39}$. Example, human (precursor): database code GLUC_HUMAN, 180 amino acids (20.89 kDa). *See also* **enteroglucagon**, **glicentin**, **glucagon receptor**, **proglucagon**.

glucagon-37 *see* **enteroglucagon**.

glucagon-like immunoreactant *abbr.*: GLI; any member of a group of peptides found in extracts of mammalian gastrointestinal tract that react with N-terminal-specific anti-glucagon antibodies. A particular component of such material may be denoted by means of a suffixed roman numeral, e.g. GLI-I, and the relative molecular mass of the component in question may be indicated by a superscript, e.g. ^{8000}GLI. The principal molecular species recorded include one of ≈12 kDa (^{12000}GLI), a second of ≈8 kDa (^{8000}GLI), and a third of ≈4.5 kDa (^{4500}GLI), the first two being the predominant forms. All have glucagon-like biological activities; e.g. they bind to glucagon receptors of liver plasma membrane, activate hepatic adenylate cyclase, and cause the release of insulin. *See also* **glicentin**, **proglucagon**.

glucagon-like insulinotropic peptide *see* **GLIP**.

glucagon-like peptide receptor any of the membrane proteins that bind glucagon-like peptides (*abbr.*: GLPs) and mediate their intracellular effects. A receptor for GLP-1 has been characterized. It is a seven-transmembrane-segment protein that is coupled to a G-protein activating adenylate cyclase. Example from human: database code GLPR_HUMAN, 463 amino acids (53.06 kDa).

glucagonoma a neoplasm (benign or malignant), originating usually from the A cells of pancreatic islets, that autonomously secretes **glucagon** or **glucagon-like immunoreactant**, frequently with associated diabetes mellitus.

glucagon receptor any of several membrane proteins that bind glucagon and mediate its intracellular effects. Activation of the liver glucagon receptor gives rise to both elevation of intracellular cyclic AMP and phosphoinositide hydrolysis with elevation of intracellular Ca^{2+}. A single clone has been isolated that, when expressed in transfected COS-7 cells, codes for a receptor that on activation can both increase cyclic AMP and intracellular Ca^{2+}, suggesting that two types of receptor may not be necessary for these two effects. This gene codes for a protein of the seven-transmembrane-segment type; database code GLR_RAT, 485 amino acids (55.04 kDa). The gene product is related to the receptors for calcitonin, parathyroid hormone, secretin, vasoactive intestinal peptide, and glucagon-like peptide I. The K_d of the expressed receptor has been found to be 20 nM (COS-7 cells) or 37 nM (BHK cells).

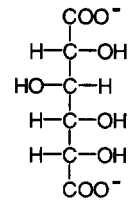
glucagon-related polypeptide *or* **glucagon-like peptide** any member of a diverse group of peptides found, e.g., in gastrointestinal tissue and blood that react with anti-glucagon antibodies and presumably contain part or all of the amino-acid sequence of **glucagon**. They include: **enteroglucagon**, **glicentin**, **glucagon-like immunoreactant**, and **proglucagon**.

glucan any glycan composed solely of glucose residues. *See also* **dextran**.

glucan 1,4-α-glucosidase EC 3.2.1.3; *other names*: glucoamylase; amyloglucosidase; α-amylase; lysosomal α-glucosidase; acid maltase; exo-1,4-α-glucosidase. An enzyme that hydrolyses terminal 1,4-α-D-glucosidic bonds (at the nonreducing end) of polysaccharides, producing β-D-glucose with inversion of the configuration. It is less active towards oligosaccharides. Some of these enzymes (including the example) have a raw-starch binding domain. The enzyme from *Aspergillus niger* is used commercially in production of glucose. Example (precursor) from *Neurospora crassa*: database code S36364, 626 amino acids (66.50 kDa); this is a good example of a protein with a **kex2** site. *See also* **glucosidase**.

α-glucan phosphorylase a **phosphorylase** with affinity for α-glucans. Example (precursor) from potato chloroplasts: database code PHSL_SOLTU, 966 amino acids (109.38 kDa); this is the L-isoform.

glucarate **1** the dianion of glucaric acid, the **aldaric acid** derived from either glucose or gulose. There are two enantiomers L- and D-glucarate; D-glucarate, *formerly known as* **saccharate**, is derived from either D-glucose or L-gulose (and vice versa for L-glucarate). **2** any salt or ester of glucaric acid.



D-glucarate

glucemia *or (esp. UK)* **glucaemia** *an alternative term for* **glycemia**.

glucitol *see* **sorbitol**.

gluco+ *or (sometimes before a vowel)* **gluc+** *comb. form* indicating glucose. *See also* **glyco+** (def. 2).

gluco- *prefix (in chemical nomenclature)* indicating a particular configuration of a set of (usually) four contiguous CHOH groups as in the acyclic forms of D- or L-glucose. *See* **monosaccharide**.

glucoamylase *another name for* **glucan 1,4-α-glucosidase**.

β-glucocerebrosidase *see* **glucosylceramidase**.

glucoconjugate *a former term for* **glycoconjugate**.

glucocorticoid *or* **glucocorticosteroid** any naturally occurring or synthetic hormonal **corticosteroid** that acts primarily on carbohydrate and protein metabolism, e.g. by promoting hepatic glycogen deposition, and that has an anti-inflammatory effect. Glucocorticoids are produced in the middle layer (zona fasciculata) of the adrenal cortex, and include **cortisol**, **corticosterone**, and **cortisone**. In the rat, corticosterone is the major product; in humans and most other mammalian species, cortisol is the major product – in humans it is secreted at a rate of ≈8–25 mg per day, compared with corticosterone at 1–4 mg per day. Glucocorticoid secretion is enhanced during stress, including hypoglycemia, hypotension, trauma (including surgery), and illness. The main physiological actions of glucocorticoids include stimulation of liver glucose output (by both glycogenolysis and gluconeogenesis), inhibition of glucose utilization by tissues, mobilization of amino acids by breakdown of muscle protein, and mobilization of fatty acids from adipose tissue. Anti-inflammatory actions include stabilization of lysosomal membranes, preventing the release of degradative enzymes, depression of phagocytosis and suppression of **T-cell** activity, suppressing the synthesis of **interleukin-1**, and stimulating the synthesis of **lipocortin**. The actions of glucocorticoids are mediated in large part through **glucocorticoid receptor** molecules, which regulate gene transcription. *Compare* **mineralocorticoid**.

glucocorticoid receptor a mammalian **transcription factor** in-

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volved in the regulation of eukaryotic gene expression and affecting cellular proliferation and differentiation in target tissues. It is a cytosolic, soluble glucocorticoid-binding protein of M_r ≈90 000, probably existing in a complex with heat-shock protein hsp90, the total complex mass being about 300 kDa. Binding of steroid induces DNA-binding function and translocation to the nucleus where the receptor–steroid complex interacts with DNA at a **glucocorticoid response element** to regulate gene transcription. Cloning and other studies have indicated the presence of a glucocorticoid-binding site in the C-terminal region (beyond residue 527 in the human protein), with a DNA-binding region in mid-molecule with two **zinc fingers** (residues 421–481). There is also a modulating N-terminal domain. There are two forms (α, β), which differ only in their C-terminal sequences; they are probably generated by alternative splicing of a single gene. The human receptor cDNA sequence predicts a more abundant 777-residue α form, and a 742-residue β form, which have identical sequences up to residue 727. The glucocorticoid receptor is similar to other steroid/thyroid/retinoic nuclear hormone receptors. Example, α form (human): database code GCRA_HUMAN, 777 amino acids (85.56 kDa).

glucocorticoid response element *abbr.*: GRE; a specific regulatory DNA sequence involved in mediating the effects of glucocorticoids on gene transcription through interaction with the activated glucocorticoid receptor. As yet it is not well characterized, but it is likely that there are a number of GREs, probably ***trans*-acting**. A consensus sequence for one such GRE is the almost palindromic structure GGTACAnnnTGTTCT.

glucocortin a protein, M_r 17 000, induced by glucocorticoids in adipocytes, liver, fibroblasts, and thymus, and common to all glucocorticoid target cells examined.

glucogenesis the production of glucose in an organism, especially from noncarbohydrate precursors.

glucogenic describing a substance, some or all the carbon atoms of which can be used to produce glucose in an organism. In particular, a glucogenic amino acid is any amino acid that gives rise to increased urinary glucose excretion when fed to a diabetic animal.

glucokinase **1** *the recommended name for* the enzyme ATP: D-glucose 6-phosphotransferase (EC 2.7.1.2), which catalyses the phosphorylation by ATP of D-glucose to D-glucose 6-phosphate with release of ADP. The enzyme occurs in invertebrates and microorganisms. Unlike **hexokinase**, which will catalyse the same reaction, it is highly specific for D-glucose. **2** *a name frequently applied to* an isoenzyme of hexokinase (EC 2.7.1.1) that is characteristic of mammalian liver.

glucon *or (formerly)* **glucone** any **glycon** in which the sugar involved is glucose.

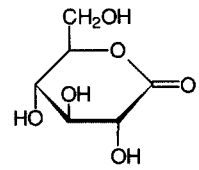
gluconate **1** the anion of **gluconic acid**. **2** any salt or ester of gluconic acid.

gluconeogenesis the metabolic formation of carbohydrates from non-carbohydrate organic precursors in liver. Formerly the term was restricted to the metabolic formation of glucose from noncarbohydrate precursors. Physiologically, an important source of precursor molecules is amino acid released from muscle protein during fasting. This is under hormonal control, especially by glucocorticoids. Alanine is an important precursor, and there is extensive conversion in muscle of other amino acids to alanine, which is then transported to the liver, where it undergoes transamination to form pyruvate. *See also* **gluconeogenic pathway**.

gluconeogenic pathway the pathway in liver by which noncarbohydrate precursors are converted to glucose 6-phosphate and thence to glucose or other carbohydrates. Precursor molecules must first be converted to pyruvate, thence successively to oxaloacetate, phosphoenolpyruvate, 2-phosphoglycerate, 3-phosphoglycerate, 1,3-bisphosphoglycerate, glyceraldehyde 3-phosphate plus glycerone phosphate, fructose 1,6-bisphosphate, fructose 6-phosphate, glucose 6-phosphate, and glucose (or other sugars). The enzymes involved are in many cases the same as those involved in the corresponding reverse step in the **glycolytic pathway**. The enzymes specific to the gluconeogenic pathway are pyruvate carboxylase, phospho*enol*pyruvate carboxykinase, fructose 1,6-bisphosphatase and glucose 6-phosphatase (see individual entries for each enzyme). The pathway is hormonally regulated, especially by glucagon, which increases cyclic AMP levels, thereby stimulating protein kinase activity. Control is effected by phosphorylation of liver pyruvate kinase, which inactivates the enzyme and thus restricts glycolysis, and phosphorylation of phosphofructokinase-2, which converts its action to that of a phosphatase which hydrolyses the 2-phosphate of fructose 2,6-bisphosphate, thereby inactivating phosphofructokinase.

gluconic acid the aldonic acid derived from glucose.

gluconolactone *the trivial name for* the γ-lactone (D-glucono-1,4-lactone) or δ-lactone (D-glucono-1,5-lactone) of D-gluconic acid.



D-glucono-1,5-lactone

glucophore the pharmacophore, or common structural feature, postulated to be present in molecules of all substances, whether chemically related or not, that possess a sweet taste, and thus to confer sweetness on them. The essential components of the glucophore are considered to be a polarized bond A–H (e.g. O–H in a sugar or N–H in a sweet amino acid), an electronegative atom B (typically =O), and a polarizable hydrophobic group X (such as H or Cl). The approximate distances between them are: A–B, 260 pm; A–X, 350 pm; B–X, 550 pm. The groups A–H and B are considered to bind respectively to similar B and A–H groups in the receptor, and the group X to bind to the receptor by charge-transfer or dispersion bonding.

glucoprotein *a former name for* **glycoprotein**.

glucosaccharase *the trivial name for* any **saccharase** that attacks the glucose end of appropriate oligosaccharides, liberating glucose.

glucosamine *symbol*: Glc*p*N; *the trivial name for* the aminodeoxysugar 2-amino-2-deoxyglucopyranose; there are two enantiomers. D-Glucosamine (*symbol*: D-Glc*p*N), *formerly known as* **chitosamine**, occurs in combined form in chitin, in mucoproteins, and in mucopolysaccharides, and is one of the most abundant natural monosaccharides.

glucosamine *N*-acetyltransferase EC 2.3.1.3; *other name*: glucosamine acetylase; an enzyme forming *N*-acetyl-D-glucosamine from acetyl-CoA and D-glucosamine while releasing CoA.

glucosamine-6-phosphate isomerase EC 5.3.1.10; *systematic name*: D-glucosamine-6-phosphate ketol-isomerase (deaminating). An enzyme that catalyses the hydrolysis of D-glucosamine 6-phosphate to D-fructose 6-phosphate and NH_3. The amino-acid sequences of bacterial and fungal types are similar. Example from *Escherichia coli*: database code NAGB_ ECOLI, 266 amino acids (29.74 kDa); 3-D structure known.

glucosaminic acid *the common biochemical name for* 2-amino-2-deoxygluconic acid.

glucosan **1** *an obsolete name for* **glucan**. **2** *an old trivial name* (established by usage but not recommended) *for* 1,6-anhydroglucopyranose.

glucose *symbol*: Glc; *the trivial name for* the aldohexose *gluco*-hexose; there are two enantiomers, D- and L-glucose. D-(+)-Glucose (symbol: D-Glu), commonly known as glucose, and formerly known as **grape sugar** or **corn sugar**, is dextrorotatory, hence also formerly (and sometimes still) known as **dextrose**; it is 0.74 times as sweet as sucrose. Aged aqueous

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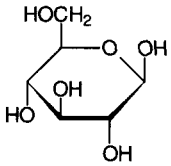
solutions of D-glucose contain an equilibrium mixture of α-D-glucopyranose, β-D-glucopyranose, and the open-chain form (*see also* **mutarotation**), whereas in crystals α-D-glucopyranose monohydrate is the stable form below 50 °C. Combined D-glucose may have either the α or the β configuration, but is invariably in the pyranose form. D-Glucose is an important source of energy for living organisms. It is found free in fruits and other parts of plants, in honey, and in animals, especially in the blood (≈5 mM in human blood). In combined form it occurs in many homo- and hetero-oligosaccharides and polysaccharides, especially in the animal storage polysaccharide glycogen and in the plant storage polysaccharides cellulose and starch.



β-D-glucose

glucose–alanine cycle *or* **alanine cycle** a metabolic cycle in which alanine is formed peripherally, e.g. in muscle, by transamination of glucose-derived pyruvate, and is transported to the liver where its carbon skeleton is reconverted to glucose.

glucose-assimilation coefficient *symbol*: *K*; *see* **glucose-tolerance test**.

glucose-dependent insulinotropic peptide *or* **glucose-dependent insulin-releasing peptide** *see* **gastric inhibitory peptide**.

glucose effect the ability of glucose in the growth medium to inhibit the synthesis of certain enzymes in bacteria growing on the medium. *See also* **catabolite repression**.

glucose fatty-acid cycle a concept to explain how changes in plasma levels of glucose and fatty acids influence one another so as to provide a homeostatic control mechanism. Its essential features are: (1) the release, for oxidation, of fatty acids from muscle or adipose tissue acylglycerols restricts glucose metabolism in muscle; and (2) glucose uptake by muscle or adipose tissue restricts the release of fatty acids from acylglycerols in these tissues. The cycle thus provides a primitive, hormone-independent mechanism tending to maintain a constant plasma glucose level in animals that feed intermittently. Insulin modifies this mechanism by enhancing glucose uptake by muscle and adipose tissue, inhibiting fatty-acid release by adipose tissue, and increasing fatty-acid esterification in both muscle and adipose tissue.

glucose isomerase a bacterial enzyme preparation that catalyses the reaction:

D-glucose = D-fructose.

It is used on a large scale in industry to convert glucose-containing materials to the much sweeter mixture of glucose plus fructose. The enzymes are usually immobilized on a variety of supports. The product is known as **high-fructose corn syrup** and is widely used as a sweetening agent. No enzyme for which this is the main function has been isolated. EC 5.3.1.18 (glucose isomerase) is now a deleted entry.

glucose oxidase EC 1.1.3.4; *other names*: glucose oxyhydrase; notatin; *systematic name*: β-D-glucose:oxygen 1-oxidoreductase; a flavoprotein (FAD) enzyme that catalyses the oxidation by dioxygen of β-D-glucose to D-glucono-1,5-lactone and H_2O_2. It has application in the experimental determination of glucose concentration (e.g. in medicine) and has some industrial uses. Example from *Aspergillus niger*: database code NRL_1GAL, 581 amino acids (63.00 kDa); 3-D structure known.

glucose-1-phosphatase EC 3.1.3.10; *systematic name*: D-glucose-1-phosphate phosphohydrolase. An enzyme that catalyses the hydrolysis of D-glucose 1-phosphate to D-glucose and orthophosphate. Example (precursor) from *Escherichia coli*: database code AGP_ECOLI, 413 amino acids (45.63 kDa).

glucose-6-phosphatase EC 3.1.3.9; *systematic name*: D-glucose-6-phosphate phosphohydrolase. An enzyme that catalyses the hydrolysis of D-glucose 6-phosphate to D-glucose and orthophosphate. It has rather wide specificity. It is the final enzyme in the **gluconeogenic pathway**. Example from mouse: database code U00445, 357 amino acids (40.43 kDa).

glucose-6-phosphatase deficiency *see* **glycogen storage disease**.

glucose-6-phosphate dehydrogenase *abbr.*: G6PDH *or (in clinical chemistry)* GPD; EC 1.1.1.49; *recommended name*: glucose-6-phosphate 1-dehydrogenase; *systematic name*: D-glucose-6-phosphate:$NADP^+$ 1-oxidoreductase; *other name (obsolete)*: Zwischenferment. An enzyme that catalyses the conversion of D-glucose 6-phosphate and $NADP^+$ to D-glucono-1,5-lactone 6-phosphate and NADPH. This is an early step in the **pentose phosphate pathway** and the **Entner–Doudoroff pathway**, and thus in **heterolactic fermentation**. The enzyme has the greatest known variability of all enzymes in humans. Molecular variants that result in deficient activity are associated with a drug-induced hemolytic anemia, **favism**. This arises because the enzyme is involved in maintaining reduced glutathione in red cells. Example from *Drosophila melanogaster*: database code G6PD_DROME, 523 amino acids (60.05 kDa). *See also* **glucose-6-phosphate dehydrogenase deficiency**.

glucose-6-phosphate dehydrogenase deficiency a hereditary X-linked deficiency of **glucose-6-phosphate dehydrogenase** that affects mostly males. It is associated with a hemolytic anemia, but also confers some protection against malaria, since the parasite is unable successfully to pass through the schizont stage in red cells lacking this enzyme activity; hence there is a particularly high incidence in tropical Africa and the Middle and Far East. Lack of the enzyme in red cells results in failure to reduce $NADP^+$ to NADPH in adequate amounts (the **pentose phosphate pathway** playing a major role in this in the red cell), as a result of which oxidized glutathione cannot be reduced by **glutathione reductase**. Consequently, there can be hemolysis, as hemoglobin is not maintained in the ferrous state and the peroxides produced as a result of drug action promote red-cell destruction. The antimalarial drug **primaquine** and related compounds generate oxidative stress, and during World War II their administration led to the discovery of the condition in many service personnel. The multi-allelic nature of the gene has led to many investigations of its distribution. *See also* **favism**.

glucose-6-phosphate isomerase *abbr. (in clinical chemistry)*: GPI; EC 5.3.1.9; *systematic name*: D-glucose-6-phosphate ketol-isomerase; *other names*: phosphoglucose isomerase; phosphohexose isomerase; phosphohexomutase; oxoisomerase; hexosephosphate isomerase; phosphosaccharomutase; phosphoglucoisomerase; phosphohexoisomerase. An enzyme of the glycolytic pathway that catalyses the interconversion of glucose 6-phosphate and fructose 6-phosphate. Example from *Escherichia coli*, homodimer: database code G6PI_ECOLI, 549 amino acids (61.45 kDa).

glucose-tolerance curve the curve relating blood glucose concentration to time that is obtained in a **glucose-tolerance test**, either oral or intravenous.

glucose-tolerance factor *abbr.*: GTF; a water-soluble, relatively stable organic chromium complex of M_r ≈500 that is believed to be required in the diet for normal glucose tolerance in animals, including humans. It is a coordination complex between chromium (III) ions, nicotinate, glycine, glutamate, and cysteine or glutathione.

glucose-tolerance test any procedure designed to assess the response of an individual to a loading dose of glucose, widely used in the diagnosis of diabetes mellitus. The standard **oral**

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glucose tolerance test is performed in the morning following at least 3 days' unrestricted diet, physical activity, and freedom from medication. The subject should have fasted for 12 hours before the test and remain seated and non-smoking during the test. After collection of the fasting blood sample, 75 g (or 1.75 g per kg of body weight for children) glucose is ingested in 5 minutes in 200–500 mL water (formerly loads of 50 g and 100 g glucose were used). Blood samples are then collected at 30-minute intervals for 2 hours, and urine samples are collected at 0, 1, and 2 hours. All samples are assayed for glucose. For capillary blood samples, a maximum glucose level below 10 mmol L^{-1} (180 mg/100 mL) and a 2-hour value less than 7.5 mmol L^{-1} (135 mg/100 mL) are the criteria for normality. If venous blood is used the corresponding values are 8.9 mmol L^{-1} (160 mg/100 mL) and 6.1 mmol L^{-1} (110 mg/100 mL). The urine samples should be glucose free. The **intravenous glucose tolerance test** may be used when abnormal carbohydrate absorption from the gut is suspected. A common procedure for this test is to take a fasting blood sample and further samples at 10-minute intervals for 1 hour following intravenous injection of 50 mL of 50% w/v glucose solution over a period of 2 minutes. Glucose is assayed in the blood samples and the logarithms of the values are plotted against time. The slope of the resulting straight line, multiplied by 100, is the **glucose-assimilation coefficient**, ***K***, which represents the percentage fall in blood glucose per minute. Values of *K* in excess of 1.1 per cent per minute are taken as normal.

glucose transporter any sugar-transport protein for which glucose is a substrate. Apart from certain ABC types (e.g. in *Escherichia coli*) many glucose transporters belong to the 12-helix superfamily of integral transmembrane proteins. They resemble one another and also the typically sugar–H^+ symport proteins of bacteria even though the mammalian examples are usually facilitated diffusion proteins. Examples from human; type 1 (erythrocyte and brain): database code GTR1_HUMAN, 492 residues (54.15 kDa); type 4 (insulin responsive, muscle and brown fat): database code GTR4_HUMAN, 509 amino acids (54.72 kDa). The latter is a candidate for the factor responsible for certain post-receptor defects in non-insulin-dependent diabetes mellitus. *See also* **sugar transporter**.

glucosidase any **glycosidase** that hydrolyses *O*-glucosyl-, *N*-glucosyl-, or *S*-glucosyl-compounds.

***α*-Glucosidase** EC 3.2.1.20; *systematic name:* α-D-glucoside glucohydrolase; *other names:* maltase; glucoinvertase; glucosidosucrase; maltase–glucoamylase. An enzyme that hydrolyses maltose and terminal (nonreducing end) 1,4-α-D-glucosidic bonds of oligosaccharides to yield α-D-glucose with retention of configuration. Maltases from some sources (especially intestine) act also on polysaccharides and may slowly hydrolyse (1→6)-α-D-glucosidic linkages as well. Most active with oligosaccharides, the enzyme catalyses the final step in the degradation of starch and is widely distributed in plants. Example (precursor) from the yeast *Candida tsukubaensis*: database code AGLU_CANTS, 1070 amino acids (118.50 kDa). *See also* **glucan 1,4-α-glucosidase**.

***β*-Glucosidase** EC 3.2.1.21; *systematic name*: β-D-glucoside glucohydrolase; *other names*: cellobiase; gentiobiase. An enzyme that hydrolyses terminal (nonreducing end) 1,4-β-D-glucosidic bonds to yield β-D-glucose with retention of configuration. Example (precursor) from the yeast *Kluyveromyces marxianus*: database code bglsKLUMA, 845 amino acids (93.81 kDa).

glucoside *or (formerly)* **glycoside** any **glycoside** (def. 1) in which the sugar moiety is a glucose residue.

glucosuria the presence of glucose in the urine. It is sometimes loosely referred to by the older term **glycosuria**, which now strictly implies the presence of any type of sugar in urine. Glucosuria occurs in **diabetes mellitus** and is diagnostically important. It may also occur because of renal defects, as in **Fanconi syndrome**. *See also* **fructosuria**.

glucosyl any glycosyl group formed by detaching the anomeric hydroxyl group, on C-1, from a cyclic form (pyranose or furanose) of glucose or a glucose derivative.

glucosylated hemoglobin *a misnomer for* **glycated hemoglobin**.

glucosylation **glycosylation** with one or more glucosyl groups. —**glucosylated** *adj.*

glucosylceramidase EC 3.2.1.45; *other names*: β-glucocerebrosidase; acid β-glucosidase; *systematic name*: D-glucosyl-*N*-acylsphingosine glucohydrolase; a lysosomal enzyme that catalyses the hydrolysis of D-glucosyl-*N*-acylsphingosine to D-glucose and *N*-acylsphingosine. A deficiency of this enzyme is the cause of **Gaucher's disease**, in which there is an accumulation of glucocerebroside. Example (precursor) from human: database code GLCM_HUMAN 536 amino acids (59.63 kDa).

glucosylceramide *the recommended term for* any D-glucosyl-*N*-acylsphingosine, i.e. any **cerebroside** in which the sugar moiety is D-glucose.

glucosyloxy any of the glycosyloxy groups formed by detaching the hydrogen atom from the anomeric hydroxyl group, on C-1, from a cyclic form (pyranose or furanose) of glucose.

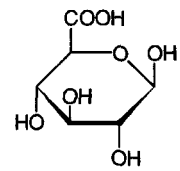
glucosyltransferase any hexosyltransferase enzyme (EC 2.4.1) for which the glycosyl group transferred is glucosyl. The acceptor may be orthophosphate (as for e.g. **phosphorylase**), but more often is another carbohydrate molecule (as for e.g. **glycogen synthase**) and sometimes a lipid (as in the synthesis of 3-D-glucosyl-1,2-diacylglycerol). *See also* **B-transferase**, **lactose synthase**, **Lewis transferase**.

glucuronate **1** the anion of glucuronic acid. **2** any salt or ester of glucuronic acid.

glucuronate pathway *or* **glucuronate oxidation pathway** the metabolic pathway by which D-glucuronate is converted, via L-gulonate, L-xylulose, xylitol, and D-xylulose, to D-xylulose 5-phosphate, an intermediate in the pentose phosphate pathway. In **essential pentosuria** there is defective conversion of L-xylulose to xylitol. In a side branch of the pathway L-ascorbate is formed, via L-gulonolactone, from L-gluconate. Primates and the guinea pig lack the ability to convert L-gulonolactone to L-ascorbate (*see* **ascorbic acid**).

glucuronate reductase EC 1.1.1.19; *systematic name*: L-gulonate:$NADP^+$ 6-oxidoreductase. An enzyme that reduces the aldehyde group at C-1 of D-glucuronate thus forming L-gulonate. *See* **glucuronate pathway**.

glucuronic acid *abbr. (sometimes):* GA; *symbol:* GlcA (*or (formerly)* GlcU *or* GlcUA); the uronic acid formally derived from glucose by oxidation of the hydroxymethylene group at C-6 to a carboxyl group. There are two enantiomers; D-glucuronic acid is widely distributed in plants and animals, where it usually occurs as glucuronides.



β-D-glucuronic acid

***β*-glucuronidase** *abbr. (in clinical chemistry):* GRS; EC 3.2.1.31, an enzyme that catalyses the hydrolysis of a β-D-glucuronoside to D-glucuronate and the corresponding hydroxy compound, which may be an alcohol, a phenol, or a saccharide. Deficiency of β-glucuronidase occurs in human type VII mucopolysaccharidosis. It is a homotetramer, and a lysosomal enzyme. Example (precursor) from human: database code BGLR_HUMAN, 651 amino acids (74.63 kDa).

glucuronide *former name for* **glucuronoside**.

glucuronoside *or (formerly)* **glucuronide** any compound formed by combination in (α or β) glycosidic linkage of a hydroxy compound with the anomeric carbon atom of glu-

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curonate. The hydroxy compound may be a saccharide, an alcohol, or a phenol. β-D-Glucuronosides are formed in so-called **detoxication** reactions.

glucuronosyl the glycosyl group formed by removal of the anomeric hydroxyl group from glucuronic acid or glucuronate.

glucuronosyltransferase *another name for* **UDPglucuronosyltransferase**.

glucuronoyl the univalent acyl group derived from glucuronic acid.

glued *see* **dynactin**.

Glu(NH_2) *(formerly) symbol for* a residue of the α-amino acid L-glutamine (Gln or Q now recommended).

Glu-NH_2 *symbol for* a residue of the α-amino acid L-isoglutamine.

Glu(OEt) *symbol for* a residue of γ-ethyl glutamate; O^5-ethyl hydrogen glutamate.

Glu-OEt *symbol for* a residue of α-ethyl glutamate; O^1-ethyl hydrogen glutamate.

GluR receptor *see* **glutamate receptor**.

GLUT *an abbr. commonly used for* **glucose transporter**.

glutaconyl-CoA decarboxylase EC 4.1.1.70; an enzyme that catalyses the decarboxylation of glutaconyl-CoA (pent-2-enoyl-CoA) to but-2-enoyl-CoA, releasing CO_2. Biotin is a coenzyme. The enzyme is dependent on Na^+, and functions as a sodium pump in the bacterial membrane.

glutamate **1** *(in biochemistry)* glutamate(1–); glutamic-acid monoanion; hydrogen glutamate. In theory, the term denotes any ion or mixture of ions formed from **glutamic acid** and having a net charge of –1, although the species $^-OOC–[CH_2]_2–CH(NH_3^+)–COO^-$ generally predominates in practice. **2** *(in chemistry) the systematic name for* glutamate(2–); glutamic-acid dianion. **3** any salt containing an anion of glutamic acid. **4** any ester of glutamic acid.

glutamate *N*-acetyltransferase EC 2.3.1.35; *other names*: ornithine acetyltransferase; ornithine transacetylase; an enzyme of the pathway in bacteria for the formation of ornithine from glutamate. It catalyses a reaction between N^2-acetyl-L-ornithine and L-glutamate to form L-ornithine and *N*-acetyl-L-glutamate (*abbr.*: AGA). In bacteria, AGA is then converted to *N*-acetylglutamate 5-semialdehyde, which undergoes transamination to N^2-acetylornithine. Example from *Bacillus stearothermophilus*: database code ARGJ_BACST, 410 amino acids (43.33 kDa); this is a bifunctional enzyme (*other name*: AGS/OCTase) containing activities for this and also **amino-acid *N*-acetyl transferase**.

glutamate–ammonia ligase EC 6.3.1.2; *systematic name:* L-glutamate:ammonia ligase (ADP-forming); *other name:* glutamine synthetase. An enzyme that catalyses a reaction between ATP, L-glutamate, and NH_3 to form ADP, orthophosphate, and L-glutamine. This is the first step in the fixation of ammonia in plants, the ATP-dependent incorporation of NH_4^+ into the amide position of glutamine. The second step involves L-glutamate synthase (ferredoxin) and the combined effect of the two enzymes is to produce L-glutamate from 2-oxoglutarate and ammonium (NH_4^+), a major NH_4^+ assimilatory route. Glutamate–ammonia ligase has a molecular mass of 33 kDa and its eight monomers are arranged in two parallel tetramers. Example from *Escherichia coli*: 12 subunits in two hexagons, database code GLNA_ECOLI, 468 amino acids (51.71 kDa). The activity is controlled by adenylylation in the presence of ATP by **[glutamate-ammonia-ligase] adenylyl transferase** to adenylate a tyrosine residue; the fully substituted enzyme is inactive; transcription is regulated by **nitrogen regulatory protein**.

[glutamate–ammonia-ligase] adenylyltransferase EC 2.7.7.42; *other name*: glutamine-synthetase adenylyltransferase; an enzyme that catalyses the adenylylation of [L-glutamate:ammonia ligase (ADP-forming)] by ATP to form adenylyl-[L-glutamate:ammonia ligase (ADP-forming)] with release of pyrophosphate. The adenylylation regulates enzyme activity (*see* **glutamate–ammonia ligase**). Example from *Escherichia coli*: database code GLNE_ECOLI, 945 amino acids (108.15 kDa).

glutamate/aspartate transporter any membrane protein that transports glutamate and aspartate. Two types are known. (1) An H^+-symport protein of the bacterial (inner) membrane; it is probably a 12-helix integral membrane protein. Although Na^+ is not involved, there is a sequence resemblance to the second type (below). Example from *Escherichia coli*: database code GLTP_ECOLI, 437 amino acids (47.10 kDa). (2) The sodium-dependent transporter of brain; it is similar to sodium-dicarboxylate symporters. Putatively it is a glycosylated integral membrane protein of brain (high levels in Purkinje cell layer). Example from rat: database code GLT1_RAT, 573 amino acids (62.03 kDa).

glutamate–cysteine ligase EC 6.3.2.2; *other name*: γ-glutamylcysteine synthetase; an enzyme of the pathway for the formation of glutathione. It catalyses the formation of γ-L-glutamyl-L-cysteine from ATP, L-glutamate, and L-cysteine with release of ADP and orthophosphate. Example from *Escherichia coli*: database code GSH1_ ECOLI, 518 amino acids (58.18 kDa).

glutamate dehydrogenase EC 1.4.1.2; *systematic name*: L-glutamate:NAD^+ oxidoreductase (deaminating). An enzyme that catalyses the reaction:

$$\text{L-glutamate} + H_2O + NAD^+ = \text{2-oxoglutarate} + NH_3 + NADH.$$

This oxidative removal of the amino group from glutamate avoids the need for an oxo-acid acceptor, and in **ureotelic** animals is a major route for the removal of nitrogen as NH_4^+, which is then converted to urea in the **ornithine–urea cycle**. Example from *Neurospora crassa*: database code DHE2_ NEUCR, 1026 amino acids (115.52 kDa). Example from yeast, homotetramer: database code DHE2_YEAST, 1092 amino acids (124.19 kDa). *See also* **glutamate dehydrogenase (NADP+)**.

glutamate dehydrogenase ($NADP^+$) EC 1.4.1.4; *systematic name*: L-glutamate:$NADP^+$ oxidoreductase (deaminating). An enzyme that catalyses the oxidation by $NADP^+$ of L-glutamate to form 2-oxoglutarate, NH_3, and NADPH. Two forms exist. One is a homotetramer. Example from *Neurospora crassa*: database code DHE2_NEUCR, 1026 amino acids (115.52 kDa). The other form, found in bacteria and plants, mainly proceeds in the direction of glutamate synthesis, as an NH_3-assimilatory enzyme. It is the product of the *am* gene, and is a homohexamer. Isoforms of this enzyme provided the first demonstration of **interallelic complementation**. Example from *Neurospora crassa*: database code DHE4_NEUCR, 453 amino acids (48.67 kDa).

glutamate–oxaloacetate transaminase *see* **aminotransferase**.

glutamate–pyruvate transaminase *see* **aminotransferase**.

glutamate receptor *abbr.*: GluR; any of a number of membrane proteins that bind glutamate and mediate its effects in neurotransmission. A major subdivision within glutamate receptors is between those (ionotropic) that act as ligand-gated ion channels and those (metabotropic) that are coupled to G-proteins. **Ionotropic GluR receptors** are further subdivided into three classes, named after dicarboxylic amino acids that act as agonists: (1) *N*-methyl-D-aspartate (NMDA) receptors; they play a key role in memory acquisition, learning, and neurological disorders and are the target for **conantokin-G**; (2) α-amino-3-hydroxy-5-methyl-4-isoxalone (**AMPA**) receptors, formerly designated quisqualate receptors; and (3) kainate receptors. Most of the fast excitatory synaptic transmission in the vertebrate central nervous system is mediated by GluR channels. There are many molecular subtypes of GluR in these categories; however, in all ionotropic receptors an ion channel is an intrinsic property of the receptor structure, generally with a broad ionic selectivity to monovalent ions; NMDA channels are also five to ten times more permeable to Ca^{2+} ions than to Na^+ or K^+ ions. The sequences of the subunits of these recep-

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tors reveal four putative transmembrane segments; these subunits have been designated α, β, γ, δ, ε, and ζ. The members of the α subfamily constitute AMPA-selective GluR channels; the β and γ subfamilies include the subunits of the kainate-selective GluR channel; NMDA receptor channels are composed of εζ heteromers. Example of an ionotropic receptor (precursor) from rat: database code JN0339, 885 amino acids (99.34 kDa). **Metabotropic GluR receptors** (mGluR) that have been cloned include $mGluR_1$, of which two alternatively spliced versions exist (1199 and 906 amino acids), and $mGluR_2$ (872 amino acids); both of these types have seven transmembrane segments. The activity of this receptor is mediated by a G-protein that activates a phosphatidylinositol–Ca^{2+} second messenger system. Example, receptor 1 (precursor) from rat, transmembrane glycoprotein, seven motifs: database code MGR1_RAT, 1199 amino acids (133.08 kDa) of which amino acids 21–1199 comprise the receptor.

glutamate 1-semialdehyde glutamic α-semialdehyde; the L enantiomer, L-glutamate 1-semialdehyde, (*S*)-4-amino-5-oxopentanoate, is the precursor of 5-aminolevulinate (*see* **glutamate-1-semialdehyde 2,1-aminomutase**). It is synthesized in plants from glutamate bound to a specific tRNA; after reduction of the 1-carboxyl group, the tRNA is removed to yield glutamate 1-semialdehyde. *Compare* **glutamate 5-semialdehyde**.

glutamate 5-semialdehyde glutamic γ-semialdehyde; the L enantiomer, L-glutamate 5-semialdehyde, (*S*)-2-amino-5-oxopentanoate, is an intermediate in the synthesis of proline from ornithine. In plants and bacteria it is formed in a pathway in which L-glutamate is first converted to *N*-acetyl-L-glutamate, which is reduced to *N*-acetyl-L-glutamate 1-semialdehyde, from which the acetyl group is then removed. In animals it is formed from ornithine by transamination of the δ-amino group. *See* **proline**. *Compare* **glutamate 1-semialdehyde**.

glutamate-1-semialdehyde 2,1-aminomutase EC 5.4.3.8; *other name*: glutamate-1-semialdehyde aminotransferase. The enzyme synthesizing 5-aminolevulinate in plants; it catalyses the conversion of (*S*)-4-amino-5-oxopentanoate (i.e. **glutamate 1-semialdehyde**) to 5-aminolevulinate. Example from *Escherichia coli*: database code GSA_ECOLI, 426 amino acids (45.42 kDa).

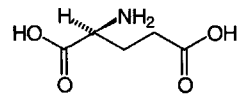
glutamate synthase (ferredoxin) EC 1.4.7.1; *systematic name*: L-glutamate:ferredoxin oxidoreductase (transaminating). An enzyme that catalyses the second step in the fixation of ammonia in plants, i.e. the transfer of the NH_2 group from the amide group of glutamine to 2-oxoglutarate to form L-glutamate. The reaction is between L-glutamine, 2-oxoglutarate, and two molecules of reduced ferredoxin; the products are two molecules of L-glutamate and two of oxidized ferredoxin. In plants the combination of the action of **glutamate–ammonia ligase** and this enzyme results in the production of one molecule of glutamate from one of 2-oxoglutarate and one of NH_4^+. *See also* **glutamate synthase (NADH)**, **glutamate synthase (NADPH)**.

glutamate synthase (NADH) EC 1.4.1.14; *systematic name*: L-glutamate:NAD^+ *oxidoreductase (transaminating)*. An enzyme that catalyses a reaction between L-glutamine, 2-oxoglutarate, and NADH to form two molecules of L-glutamate and NAD^+. FMN is a cofactor. Example from alfalfa: database code GLSN_MEDSA, 2194 amino acids (240.10 kDa).

glutamate synthase (NADPH) EC 1.4.1.13; *systematic name*: L-glutamate:$NADP^+$ oxidoreductase (transaminating). An enzyme that catalyses the formation of two molecules of L-glutamate and one of $NADP^+$ from L-glutamine, 2-oxoglutarate, and NADPH. *It is an iron–sulfur flavoprotein.* It brings together nitrogen and carbohydrate metabolism in bacteria, since in association with **glutamate–ammonia ligase** it functions as the second step in a major NH_3-assimilatory pathway. It exists as an aggregate of four heterodimers of large and small subunits; glutamine binds to the large subunit and transfers $-NH_2$ from its amido group to 2-oxoglutarate, which apparently binds to the small subunit. Example from *Escherichia coli*: small subunit, database code GLTD_ECOLI, 470 amino acids (52.09 kDa); large subunit, database code GLTB_ECOLI, 1514 amino acids (166.04 kDa).

glutamic *the general name for* a residue of glutamic acid, whether or not the γ-carboxyl group is protonated.

glutamic acid *abbr. (sometimes)*: GA; *the trivial name for* α-aminoglutaric acid; 2-aminopentanedioic acid; HOOC–$[CH_2]_2$–$CH(NH_2)$–COOH; a chiral α-amino acid. L-Glutamic acid (*symbol*: E *or* Glu), (*S*)-2-aminopentanedioic acid, is a coded α-amino acid found in peptide linkage in proteins; codon: GAA or GAG. In mammals it is a nonessential dietary amino acid and is glucogenic. Residues of D-glutamic acid (*symbol*: D-Glu *or* DGlu), (*R*)-2-aminopentanedioic acid, are found in the cell-wall material of various bacterial species and (as poly-D-glutamic acid) in the capsular substances of *Bacillus anthracis*, *B. subtilis*, and other bacteria. One residue of D-glutamic acid per molecule occurs in the antibiotic bacitracin A (*see* **bacitracin**) and also in **glutathione**.



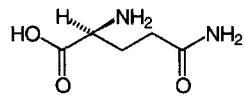
L-glutamic acid

glutamic amide **1** glutamic 1-amide (i.e. **isoglutamine**). **2** glutamic 5-amide (i.e. **glutamine**).

glutaminase EC 3.5.1.2; *other and systematic name*: L-glutamine amidohydrolase; an enzyme that catalyses the hydrolysis of L-glutamine to L-glutamate and NH_3. Example (kidney isoform) from *Rattus norvegicus*: database code GLSK_RAT, 674 amino acids (73.94 kDa).

glutaminate **1** the glutamine anion; the anion, H_2N–CO–$[CH_2]_2$–$CH(NH_2)$–COO^-, derived from glutamine. **2** any salt containing glutamine anion. **3** any ester of glutamine.

glutamine *the trivial name for* the γ-amide of glutamic acid; glutamic 5-amide; α-aminoglutaramic acid; 2-amino-4-carbamoylbutanoic acid; H_2N–CO–$[CH_2]_2$–$CH(NH_2)$–COOH; a chiral α-amino acid. L-Glutamine (*symbol*: Q *or* Gln *or (formerly)* $Glu(NH_2)$), (*S*)-2-amino-4-carbamoylbutanoic acid, is a coded α-amino acid found in peptide linkage in proteins; codon: CAA or CAG. In mammals it is a nonessential α-amino acid and is glucogenic. D-Glutamine (*symbol*: D-Gln *or* DGln), (*R*)-2-amino-4-carbamoylbutanoic acid, is not known to occur naturally. *Compare* **isoglutamine**.



L-glutamine

glutamine amidotransferase *abbr.*: GATase; *a nonsystematic name for* carbon–nitrogen ligases that employ glutamine as the amido-N-donor; i.e. members of the sub-subclass EC 6.3.5. These enzymes transfer the $-NH_2$ group from glutamine to another reactant, e.g. **GMP synthase**. The enzyme activity is also an activity associated with **CAD protein** in mammals. *See also* **glutamate synthase (ferredoxin)**, **glutamate synthase (NADH)**, **glutamate synthase (NADPH)**.

glutamine–pyruvate aminotransferase EC 2.6.1.15; *other names*: glutaminase II; glutamine–oxo-acid transaminase; glutamine transaminase L; an enzyme that catalyses the reaction:

L-glutamine + pyruvate = 2-oxoglutaramate + L-alanine.

Pyridoxal-phosphate is a cofactor. *See also* **transamination**.

glutamine synthetase *see* **glutamate–ammonia ligase**.

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glutamine-synthetase adenylyltransferase *see* **[glutamate–ammonia-ligase] adenylyltransferase**.

glutamine transaminase L *see* **glutamine–pyruvate aminotransferase**.

glutamino 1 **N^2-glutamino** the alkylamino group, H_2N–CO–$[CH_2]_2$–CH(COOH)–NH–, derived from glutamine by loss of a hydrogen atom from its α-amino group. 2 **N^5-glutamino** the acylamino group, H_2N–CH(COOH)–$[CH_2]_2$–CO–NH–, derived from glutamine by loss of a hydrogen atom from its amide group.

glutaminyl the acyl group, H_2N–CO–$[CH_2]_2$–$CH(NH_2)$–CO–, derived from glutamine. *Compare* **isoglutaminyl**.

glutamo the alkylamino group, HOOC–$[CH_2]_2$–CH(COOH)–NH–, derived from glutamic acid.

glutamoyl the diacyl group, –CO–$[CH_2]_2$–$CH(NH_2)$–CO–, derived from glutamic acid.

α-glutamyl glutam-1-yl; the α-monoacyl group, HOOC–$[CH_2]_2$–$CH(NH_2)$–CO–, derived from glutamic acid.

γ-glutamyl *or (formerly)* isoglutamyl, glutam-5-yl; the γ-monoacyl group, –CO–$[CH_2]_2$–$CH(NH_2)$–COOH, derived from glutamic acid.

glutamyl aminopeptidase EC 3.4.11.7; *other names*: aminopeptidase A; angiotensinase A; differentiation antigen gp160; an enzyme that removes an N-terminal glutamyl residue from a peptide. It can also hydrolyse N-terminal aspartase, and can thus inactivate **angiotensin** II, being expressed in kidney, as well as on cells of the capillaries and intestine, and on lymphocytes Example from human: database code AMPE_HUMAN, 957 amino acids (109.24 kDa).

γ-glutamyl cycle an integrated cycle of chemical events that uses the γ-carboxyl group of glutamate to transport amino acids actively across (mammalian) cell membranes. Glutathione supplies the activated γ-glutamyl group, which reacts by transpeptidation with the amino acid to be transported. The resulting γ-glutamylamino acid enters the cell, where it is split into the free amino acid and 5-oxoproline. The latter is then converted to glutamate in an ATP-dependent reaction. The cysteinylglycine formed from glutathione in the initial transpeptidation step is hydrolysed by a peptidase. Glutathione is then regenerated in two ATP-dependent steps. *See also* **glutamyltransferase**.

γ-glutamylcysteine synthetase *see* **glutamate–cysteine ligase**.

glutamyl endopeptidase EC 3.4.21.19; *other names*: staphylococcal serine proteinase; V8 proteinase; protease V8; endoproteinase Glu-C. An enzyme that catalyses the preferential cleavage: Asp-|-Xaa, Glu-|-Xaa. Example (precursor) from *Staphylococcus aureus*: database code STSP_STAAU, 336 amino acids (36.29 kDa).

glutamyltransferase *abbr. (in clinical chemistry)*: GMT; EC 2.3.2.2; *recommended name*: γ-glutamyltransferase; *systematic name*: (5-L-glutamyl)-peptide:amino acid 5-glutamyltransferase; *other name*: γ-glutamyl transpeptidase. An enzyme that reversibly transfers a γ-L-glutamyl residue (linked to the substrate by an isopeptide bond) from the N terminus of a peptide, normally glutathione, to the amino group of an amino acid. It is present in high concentrations in liver, kidney, prostate, and pancreas, and is useful diagnostically in liver or biliary disease, levels being five times normal or more in cholestasis, hepatitis, and cirrhosis, and also in pancreatitis; it is also elevated in the plasma of alcoholics. The level in normal human (male) plasma is <60 IU L^{-1}. *See also* **γ-glutamyl cycle**.

glutaraldehyde pentanedial; a compound that is useful as a tissue fixative in electron microscopy, as a crosslinking agent for compounds containing amino groups, and as a sporicide.

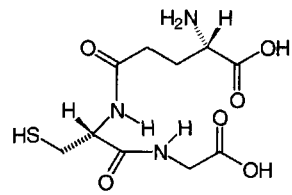
glutaramic acid *the trivial name for* 4-carbamoylbutanoic acid; H_2N–CO–$[CH_2]_3$–COOH; the monoamide of glutaric acid (*see* **glutarate**).

glutarate 1 *trivial name for* propane-1,3-dicarboxylate; pentanedioate; $^-$OOC–$[CH_2]_3$–COO^-; the dianion of glutaric acid (pentanedioic acid). 2 any mixture of free glutaric acid and its mono- and dianions. 3 any (partial or full) salt or ester of glutaric acid.

glutaredoxin a monomeric polypeptide with a similar function to **thioredoxin**. It can replace thioredoxin, or may be the main reactant, in the pathway for nucleotide reduction. Example from *Escherichia coli*: database code GLRX_ECOLI, 85 amino acids, (9.67 kDa).

glutaryl-CoA dehydrogenase EC 1.3.99.7; a flavoprotein decarboxylase that catalyses the reaction between glutaryl-CoA and acceptor to form crotonoyl-CoA, CO_2, and reduced acceptor. Example from *Pseudomonas* sp. (fragment): database code A48367, 20 amino acids (2.10 kDa).

glutathione *abbr.*: GSH; *symbol*: Glu(-Cys-Gly); γ-glutamylcysteinylglycine, a tripeptide that is widely distributed in most if not all cells. It acts as a coenzyme for some enzymes and as an antioxidant in the protection of sulfhydryl groups in enzymes and other proteins; it has a specific role in the reduction of hydrogen peroxide and oxidized ascorbate, and it participates in the **γ-glutamyl cycle**. Glutathione may be oxidized with the formation of a disulfide bridge linking two molecules and generation of the compound known as **oxidized glutathione** (*or* the oxidized form of glutathione) (*abbr.*: GSSG). For clarity, glutathione is sometimes termed **reduced glutathione** (*or* the reduced form of glutathione).



glutathione dehydrogenase (ascorbate) EC 1.8.5.1; an enzyme that restores ascorbate to its reduced state after exercise of its function of reducing agent. It catalyses the reduction by two molecules of glutathione of dehydroascorbate to form oxidized glutathione and ascorbate.

glutathione peroxidase EC 1.11.1.9; *systematic name*: glutathione:hydrogen-peroxide oxidoreductase. An enzyme that catalyses the oxidation by hydrogen peroxide of two molecules of glutathione to form oxidized glutathione and two molecules of H_2O. It has a UGA-encoded selenocysteine residue at its active site. The main role of the enzyme is to protect hemoglobin from oxidative breakdown: the oxidized glutathione is reduced by **glutathione reductase**, the system thus contributing to a reduction of peroxide levels in the cell. Example from human: database code GSHC_HUMAN, 201 amino acids (21.87 kDa).

glutathione reductase *abbr. (in clinical chemistry)*: GTD; EC 1.6.4.2; *recommended name*: glutathione reductase (NADPH); *systematic name*: NADPH:oxidized-glutathione oxidoreductase. An enzyme that catalyses the reaction:

NADPH + oxidized glutathione = $NADP^+$ + 2 glutathione.

It is a dimeric protein, has FAD as cofactor, and is important in maintaining glutathione in the reduced state. Example from *Escherichia coli*: database code GSHR_ECOLI, 450 amino acids (48.72 kDa).

glutathione synthase EC 6.3.2.3; *other name*: glutathione synthetase; an enzyme that catalyses the formation of glutathione from ATP, γ-L-glutamyl-L-cysteine, and glycine with release of ADP and orthophosphate. Example from *Escherichia coli*: database code GSH2_ECOLI, 316 amino acids (35.52 kDa); 3-D structure of parts is known.

glutathione transferase EC 2.5.1.18; *systematic name*: RX:glutathione R-transferase; *other names*: glutathione *S*-alkyltransferase; glutathione *S*-aryltransferase; *S*-(hydroxyalkyl)glutathione lyase; glutathione *S*-aralkyltransferase;

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glutathione *S*-transferase. Glutathione transferases catalyse various glutathione-dependent reactions:
(1) nucleophilic substitution, e.g.

$$RX + GSH \rightarrow RSG + HX$$

where RX is an aryl- or alkyl-halide (EC 2.5.1.18); (2) addition of GSH across activated unsaturated carbon–carbon or carbon–nitrogen bonds (often α,β-saturated ketones/thiones) or oxirane, e.g.

$$R{-}CH{-}CH_2 + GSH = R{-}CHOH{-}CH_2SG;$$

(3) organic hydroperoxide reduction (selenium-independent GSH peroxidase):

$$ROOH + 2GSH \rightarrow ROH + GSSG + H_2O;$$

(4) organic nitrite reduction

$$RONO + GSH \rightarrow GSNO + ROH;$$

(5) isomerizations in which GSH acts as cofactor, e.g. conversion of prostaglandin H to prostaglandin D. The proteins also bind a variety of hydrophobic anions, e.g. hematin, fatty acid and steroid metabolites, and various xenobiotics/metabolites including the GSH conjugates which may be their catalytic products. Such binding is responsible for their retention by S-linked GSH-Sepharose, hence the widely used simple purification of **GST fusion proteins**. GSH transferases were originally identified as binding proteins (*see* **ligandin**) and are widely distributed, abundant dimeric soluble enzymes or trimeric membrane-bound forms. They are generally considered an important part of phase II metabolism of xenobiotics. Five classes of soluble GSH transferase subunits have been distinguished (α, μ, π, θ, and σ) and heterodimers occur at least within classes yielding, for example, about 20 different isoenzymes in the rat. Distinct soluble mitochondrial and bacterial forms also occur. Example, GST 5.7 from mouse: database code GTSA_MOUSE, 222 amino acids (25.55 kDa). Example, GST 1-1 from *Drosophila melanogaster*: database code GT_DROME, 209 amino acids (23.84 kDa).

glutelin any member of a group of simple proteins found especially in the seeds of cereal plants. They are insoluble in water, dilute salt solutions, and ethanol but are soluble in dilute acids or alkalis. The group includes the **glutenins** of wheat, the hordenins of barley, and the oryzemins of rice. They serve as storage proteins, and have Gln-rich domains. Example from rice, homohexamer of subunits (acidic and basic chain derived from one precursor) with Gln-rich domains; glutelin I precursor: database code GLU1_ORYSA, 499 amino acids (56.15 kDa). *Compare* **prolamin**.

gluten a proteinaceous fraction obtained from certain cereal seeds, especially wheat, consisting of a considerable number of proteins that are all either **glutelins** or **prolamins**. It forms a sticky mass when wet, and gives dough its characteristic consistency. *See also* **celiac disease**.

glutenin any **glutelin** of the endosperm of wheat seeds. Glutenins form aggregates of high molecular mass in which they are linked together by disulfide bridges; they are thought to be responsible for the viscoelastic properties of wheat dough. The sequences contain repeats of two motifs,

GQQPGQ

and

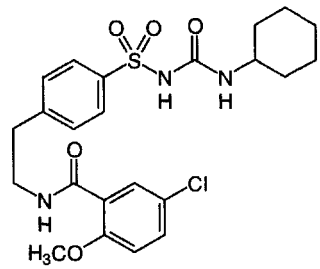
GQQPGQGQQGYYPTS.

Example, high molecular mass DY10 precursor: database code GLT0_WHEAT, 648 amino acids (69.55 kDa). *Compare* **gliadin**.

Glx *general symbol for* a residue of any α-amino (or imino) acid that yields L-glutamic acid on acid hydrolysis. It was formerly used only for either of the α-amino acids L-glutamic acid (*specific symbol*: Glu) or L-glutamine (*specific symbol*: Gln), but may now be used to represent any such residues, including those of L-4-carboxyglutamic acid (*specific symbol*: Gla) and 5-oxoproline (= pyroglutamic acid) (*specific symbol*: Glp); (alternative to Z).

Gly *symbol for* a residue of the achiral (α-)amino acid glycine (alternative to G).

glyburide 1-[[*p*-[2-(chloro-*o*-anisamido)ethyl]phenyl]sulfonyl]-3-cyclohexylurea; glibenclamide; a sulfonylurea with oral hypoglycemic actions similar to **tolbutamide**.



glyc+ *a variant form of* **glyco+** (before a vowel).

glycaemia *a variant spelling (esp. UK) of* **glycemia**.

glycamine any ω-amino-ω-deoxyalditol, i.e. any compound formally derived from an **alditol** by replacement of a terminal hydroxyl group by an amino group.

glycan *or* **polysaccharide** any polymer consisting of more than about 10 monosaccharide (i.e. glycose) residues joined to each other by glycosidic linkages. A **homoglycan** (*or* **homopolysaccharide**) is composed of only one type of monosaccharide residue, whereas a **heteroglycan** (*or* **heteropolysaccharide**) is composed of two or more different kinds of monosaccharide residue. A homoglycan is named, generally, after the constituent monosaccharide, with the +ose ending replaced by +an; hence, cellulose, dextran, dextrin, and starch are all glucans, after glucose. Distinguish from **glycosan**.

glycaric acid *an obsolescent name for* **aldaric acid**.

glycated hemoglobin *or* **glycohemoglobin** any derivative of hemoglobin that is formed nonenzymically by reaction at the N terminus with glucose. In the normal adult human such derivatives constitute a few percent of the total erythrocyte hemoglobin, the most abundant being **hemoglobin A_{1c}**, which increases severalfold in concentration in diabetes mellitus. Glycation of other proteins such as lens crystallins, collagen and low-density lipoproteins has been implicated in the pathogenesis of diabetic complications. The extent of glycation of hemoglobin is a useful measure of the degree to which the diabetes has been controlled by the administration of insulin. It is sometimes improperly termed **glucosylated hemoglobin** or **glycosylated hemoglobin**. *See also* **glycation**.

glycated proteins glycation is the post-translational modification of a protein by the covalent attachment of a sugar residue resulting from the spontaneous amino–carbonyl reaction (the **Maillard reaction**) between these two moieties. The reaction is initiated by the amino–carbonyl reaction of $-NH_2$ and $-C{=}O$ groups and occurs principally between the free amino groups of proteins and the carbonyl group of reducing sugars as first described by Louis-Camille Maillard in 1912. The initial condensation to form a Schiff's base is a spontaneous but reversible reaction that is rapidly followed by a complex series of irreversible reactions ultimately leading to the production of Amadori products of brown pigments and the cross-linking of the polypeptide chains involved. The importance of the Maillard reaction has long been recognized in the food industry where it causes spoilage and the production of colour and off-flavour in cooked foods. In 1977 Cerami identified an Amadori product in variants of human hemoglobin. Glycation of various proteins has now been implicated in the etiology of various diseases such as the development of

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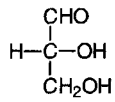
Alzheimer-type pathology. *See* **Alzheimer's disease**. *See also* **glycation**.

glycation any chemical reaction, whether enzyme-catalysed or not, that links a glycose (i.e. a sugar) to a peptide or protein and thereby forms a glycopeptide or glycoprotein. The term thus includes (enzymic or nonenzymic) **glycosylation** (and hence **glucosylation**) of a peptide or protein. However, it is usefully applied in addition to any (nonenzymic) reaction of glucose (or another sugar) with a peptide or protein where the product is not a glycoside but results from condensation of the sugar with free amino groups to form a **Schiff base** which then undergoes an **Amadori rearrangement**. —**glycated** *adj.*

glycemia *or* **glucemia** *or (esp. UK)* **glycaemia** *or* **glucaemia** **1** the presence of glucose (strictly sugar) in the blood. **2** the concentration of (strictly) sugar but, in fact, glucose in the blood. When this concentration is within normal limits the condition of the blood (or of the corresponding individual) is termed **normoglycemia**. An abnormally elevated concentration, **hyperglycemia**, may result in thirst, whereas an abnormally depressed concentration, **hypoglycemia**, may produce sweating, trembling, hunger, irritability, and in extreme cases confusion or coma. *See also* **blood sugar**, **glucose-tolerance test**, **insulin-tolerance test**. —**glycemic** *or* **glycaemic** *or* **glucemic** *or* **glucaemic** *adj.*

glyceral *an alternative name for* **glyceraldehyde**.

glyceraldehyde *symbol*: Gra; glyceral; 2,3-dihydroxypropanal; *formerly sometimes known as* **glyceric aldehyde**; *sometimes (not recommended) called* **glycerose**. It is the simplest chiral aldose and a constitutional isomer of **glycerone**. The naturally occurring form is D-glyceraldehyde, the absolute configuration of which is known and is taken as the configurational reference standard for the D-, and hence also for the L-, forms of monosaccharides.



D-glyceraldehyde

D-glyceraldehyde 3-phosphate *abbr.*: D-glyceraldehyde-3-*P*; an important intermediate in glycolysis. It is isomeric with **glycerone phosphate**.

glyceraldehyde-3-phosphate dehydrogenase (NADP$^+$) (phosphorylating) EC 1.2.1.13; *other name*: triosephosphate dehydrogenase (NADP$^+$); an enzyme that catalyses the conversion of D-glyceraldehyde 3-phosphate, orthophosphate, and NADP$^+$ to 3-phospho-D-glyceroyl phosphate and NADPH. Example (fragment) from chloroplast (spinach): database code S33872, 39 amino acids (4.46 kDa).

glyceraldehyde-3-phosphate dehydrogenase (phosphorylating) *abbr.*: GAPDH; EC 1.2.1.12; *systematic name*: D-glyceraldehyde-3-phosphate:NAD$^+$ oxidoreductase (phosphorylating); *other name*: triosephosphate dehydrogenase. An enzyme that catalyses a reaction between D-glyceraldehyde 3-phosphate, orthophosphate, and NAD$^+$ to form 3-phospho-D-glyceroyl phosphate and NADH. It is an important enzyme of the pathways of glycolysis and gluconeogenesis. It has five motifs and is a homotetramer. Example from yeast (GAPDH 1): database code G3P1_YEAST, 331 amino acids (35.56 kDa).

glycerate *symbol*: Gri; **1** 2,3-dihydroxypropanoate; $HOCH_2$–CH(OH)–COO^-; the anion derived from glyceric acid. The naturally occurring form is D-glycerate. **2** any salt or ester of glyceric acid.

glyceric aldehyde *former name for* **glyceraldehyde**.

glyceride *the former name for* **acylglycerol**; i.e. any ester of glycerol, especially the mono-, di-, or triesters of glycerol with fatty acids, formerly termed mono-, di-, or triglycerides respectively. These are now known as mono-, di-, or tri-*O*-acylglycerols.

glycerin(e) *see* **glycerol**.

glycero+ *prefix* or *infix (in chemical nomenclature)* **1** denoting a residue of glycerol. **2** denoting the acyl group derived from glyceric acid.

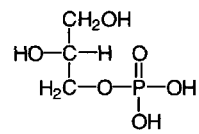
glycero- *prefix (in chemical nomenclature)* indicating the presence of a single CHOH group, in the D or L configuration as specified.

glycerokinase *see* **glycerol kinase**.

glycerol *symbol*: Gro; 1,2,3-propanetriol; a sweet, hygroscopic, viscous liquid, widely distributed in nature as a constituent of many lipids (*see* **acylglycerol**). The older name **glycerin(e)** is now obsolete except in non-technical usage and sometimes in pharmacy.

glycerol kinase EC 2.7.1.30; *systematic name*: ATP:glycerol 3-phosphotransferase; *other name*: glycerokinase. An enzyme that catalyses the phosphoryation by ATP of glycerol to form *sn*-glycerol 3-phosphate with release of ADP. In tissues and organisms ranging from human liver to microorganisms, this is the rate-limiting step in glycerol utilization. The enzyme is induced, e.g. in *Escherichia coli*, by *sn*-glycerol 3-phosphate; it is a homotetramer; example (*E. coli*): database code GLPK_ECOLI, 501 amino acids (56.04 kDa).

glycerol phosphate *or* **glycerophosphate** any of three isomeric phosphoric monoesters of glycerol; of these, two are chiral and form an enantiomeric pair, whereas the third is achiral. The earlier nomenclature of the chiral esters has been confusing; ambiguities are avoided by the adoption of **stereospecific numbering** (*symbol*: *sn*-). (1) *sn*-Glycerol 3-phosphate *or* *sn*-glycero-3-phosphate *or* 3-phospho-*sn*-glycerol *or* 3-*O*-phosphono-*sn*-glycerol (*abbr.* *sn*-glycerol-3-*P*) are alternative recommended names for the chiral ester (*R*)-[glycerol 1-(dihydrogen phosphate)]; (*R*)-[2,3-dihydroxypropyl dihydrogen phosphate]. It was previously known as L-glycerol 3-phosphate or D-glycerol 1-phosphate, and originally named D-glycerol 1-phosphate *or* L-*a*-glycerophosphate *or* L-*a*-glycerophosphoric acid. It is a component of many phospholipids. The absolute configuration is illustrated. (2) *sn*-Glycerol 1-phosphate *or* *sn*-glycero-1-phosphate *or* 1-phospho-*sn*-glycerol *or* 1-*O*-phosphono-*sn*-glycerol (*abbr.* *sn*-glycerol-1-*P*) are alternative recommended names for the chiral ester (*S*)-[glycerol 1-(dihydrogen phosphate)]; (*S*)-[2,3-dihydroxypropyl dihydrogen phosphate]. It was previously known as L-glycerol 1-phosphate *or* D-glycerol 3-phosphate, and originally named L-glycerol 1-phosphate *or* D-*a*-glycerophosphate *or* D-*a*-glycerophosphoric acid. This enantiomer is rarely encountered. (3) Glycerol 2-phosphate *or* glycero-2-phosphate *or* 2-phosphoglycerol *or* 2-*O*-phosphonoglycerol are alternative names for the achiral ester glycerol 2-(dihydrogen phosphate); di(hydroxymethyl)methyl dihydrogen phosphate. It was originally named *β*-glycerophosphate *or* *β*-glycerophosphoric acid. It is an artefact occurring in hydrolysates of glycerophospholipids that arises by migration of the phosphate group from C-1 to C-2 of the glycerol moiety. *Distinguish from* **phosphoglycerate**.



sn-glycerol 3-phosphate

glycerol-3-phosphate cycle *or* **glycerol-3-phosphate shuttle** *or* ***α*-glycerophosphate cycle** an intracellular metabolic cycle that can transfer reducing equivalents from the cytoplasm to the mitochondria. In the cytoplasm NAD-linked **glycerol-3-**

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phosphate dehydrogenase (NAD+) catalyses the reduction of glycerone phosphate (formed together with glyceraldehyde 3-phosphate in glycolysis) to *sn*-glycerol 3-phosphate. The glycerol 3-phosphate thus formed enters the mitochondria where it is oxidized to glycerone phosphate by the FAD-linked mitochondrial glycerol-3-phosphate dehydrogenase. The glycerone phosphate then returns to the cytoplasm to complete the cycle. The overall result is the oxidation of cytoplasmic NADH + H^+ to NAD^+ and the reduction of mitochondrial enzyme–FAD to enzyme–$FADH_2$.

glycerol-3-phosphate cytidylyltransferase EC 2.7.7.39; *other name*: CDPglycerol pyrophosphorylase; an enzyme that catalyses the formation of CDPglycerol from CTP and *sn*-glycerol 3-phosphate with release of pyrophosphate. Example, probable CDPglycerol pyrophosphorylase (teichoic acid biosynthesis protein D) from *Bacillus subtilis*: database code TAGD_BACSU, 129 amino acids (15.25 kDa).

glycerol-3-phosphate dehydrogenase *abbr.*: G3PDH; EC 1.1.99.5; a flavoprotein enzyme that catalyses the oxidation by an electron acceptor of *sn*-glycerol 3-phosphate to glycerone phosphate. The enzyme is part of the **glycerol 3-phosphate cycle**. Examples from *Escherichia coli* in which there are two unrelated enzymes: (1) anaerobic G3PDH, which has two subunits: database code GLPA_ECOLI, 542 amino acids (58.90 kDa); and database code GLPB_ ECOLI, 419 amino acids (45.31 kDa); (2) aerobic G3PDH: database code GLPD_ECOLI, 501 amino acids (56.69 kDa).

glycerol-3-phosphate dehydrogenase (NAD^+) EC 1.1.1.8; *systematic name*: *sn*-glycerol-3-phosphate:NAD^+ 2-oxidoreductase. An enzyme that catalyses the reaction:

sn-glycerol 3-phosphate + NAD^+ = glycerone phosphate + NADH.

Its role is especially important in the provision of glycerol 3-phosphate for lipid synthesis, using glycerone phosphate derived from glucose by the **glycolytic** pathway, and as a component of the **glycerol-3-phosphate cycle**. Example, **flightin**, homodimer from *Drosophila melanogaster*: database code GPDA_DROME, 351 amino acids (38.32 kDa).

glycerol-3-phosphate *O*-acyltransferase EC 2.3.1.15; *systematic name*: acyl-CoA:*sn*-glycerol-3-phosphate 1-*O*-acyltransferase; it catalyses the acylation by acyl-CoA of glycerol 3-phosphate to form 1-acyl-*sn*-glycerol 3-phosphate (lysophosphatidic acid) with release of CoA. This is the first step in phospholipid biosynthesis and may be involved in regulation of membrane biogenesis. Plants exhibit oleate-selective acyltransferases; the enzyme from chilling-resistant plants discriminates against palmitic acid (a fatty acid with high transition temperature), and selects oleic acid (leading to more fluid membranes), whereas the acyltransferase from sensitive plants accepts both fatty acids. Example (precursor) from pea: database code PLSB_PEA, 457 amino acids (50.70 kDa).

glycerol-3-phosphate oxidase EC 1.1.3.21; *systematic name*: *sn*-glycerol-3-phosphate:oxygen 2-oxidoreductase. An enzyme that catalyses the oxidation by dioxygen of *sn*-glycerol 3-phosphate to glycerone phosphate and hydrogen peroxide; FAD is a cofactor. It is a mitochondrial protein. In insects it plays an important role in the transfer of energy for flight, along with **glycerol-3-phosphate dehydrogenase (NAD+)** (flightin).

glycerol trinitrate *see* **trinitroglycerine**.

glycerone *symbol*: Grn; *the currently recommended trivial name for* dihydroxyacetone; 1,3-dihydroxy-2-propanone. It is the simplest ketose, is achiral, and is a constitutional isomer of glyceraldehyde.

glycerone phosphate *the currently recommended trivial name for* dihydroxyacetone phosphate; 1,3-dihydroxy-2-propanone 1-phosphate; the monoester formed by phosphorylation of dihydroxyacetone, glycerone. Glycerone phosphate and D-glyceraldehyde 3-phosphate are together described as triose phosphates and are interconvertible by triose-phosphate isomerase, EC 5.3.1.1. They are important components of the glycolytic pathway. Glycerone phosphate is a precursor of the glycerol moiety of glycerolipids.

glycerone transferase *see* **transaldolase**.

glycerophosphate *an alternative name for* **glycerol phosphate**.

***α*-glycerophosphate cycle** *an alternative name for* **glycerol-3-phosphate cycle**.

glycerophosphate phosphatidyltransferase EC 2.7.8.5; *recommended name*: CDPdiacylglycerol–glycerol-3-phosphate 3-phosphatidyltransferase. An enzyme that catalyses a reaction between CDPdiacylglycerol and *sn*-glycerol-3-phosphate to form 3-(3-*sn*-phosphatidyl)-*sn*-glycerol 1-phosphate, with release of CMP. It is a membrane protein of endoplasmic reticulum and component of the pathway for the biosynthesis of acidic phospholipids; its product loses phosphate to form phosphatidylglycerol from which **cardiolipin** is formed. Example from *Escherichia coli*: database code PGSA_ECOLI, 215 amino acids (24.64 kDa).

glycerophospholipid *general name for* any derivative of glycerophosphate that contains at least one *O*-acyl, *O*-alkyl, or *O*-alkenyl group attached to the glycerol residue. Formerly known as phosphoglyceride.

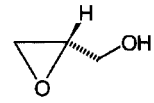
glycerophosphoric acid *see* **glycerol phosphate**.

glycerose *alternative name* (not recommended) *for* **glyceraldehyde**.

glyceroyl 2,3-dihydroxypropanoyl; the acyl group, $HOCH_2–CH(OH)–CO–$, derived from glyceric acid.

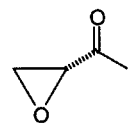
glyceryl any group derived from glycerol by replacing or removing one or more of its hydroxyl groups.

glycidol *the trivial name for* 3-hydroxypropylene oxide; 2,3-epoxy-1-propanol.



S(–)-glycidol

glycidoyl 2,3-epoxypropanoyl; the acyl group derived from glycidic acid.



(*R*)-glycidoyl group

glycidyl 2,3-epoxypropyl; the alkyl group: derived from glycidol by removal of its hydroxyl group.

glycinamide *the trivial name for* the amide of glycine, aminoacetamide; aminoethanamide; $H_2N–CH_2–CO–NH_2$. It is predominantly cationic at neutrality and is useful as a buffer substance; pK_a (20 °C) = 8.20.

glycinamide ribonucleotide synthetase (*abbr.* GARS) *see* phosphoribosylamine–glycine ligase.

glycinamide ribotide *N*-glycyl-5-phosphoribosylamine; an early intermediate in the biosynthesis of purines.

glycinate **1** glycine anion; the anion, $NH_2–CH_2–COO^–$, derived from **glycine**. **2** any salt containing glycine anion. **3** any ester of glycine.

glycine *symbol*: G *or* Gly; *the trivial name for* aminoacetic acid; aminoethanoic acid; $H_2N–CH_2–COOH$; an achiral (*α*-)amino acid and the simplest naturally occurring amino acid. It is a coded amino acid found in peptide linkage in proteins; codon: GGA, GGC, GGG, or GGU. In mammals it is a nonessential dietary amino acid and is **glucogenic**. It is

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sweet-tasting, hence its name. [From **glyc(o)+** (def. 1) + **+ine** (def. 1)]

glycine amidinotransferase EC 2.1.4.1; an enzyme that catalyses the formation of guanidinoacetate, a precursor of **creatine**, from L-arginine and glycine, also forming L-ornithine. Example (precursor) from human: database code S41734, 423 amino acids (48.40 kDa).

glycine hydroxymethyltransferase EC 2.1.2.1; *systematic name*: 5,10-methylenetetrahydrofolate:glycine hydroxymethyltransferase; *other names*: serine hydroxymethylase; threonine aldolase; serine aldolase. An enzyme that catalyses the reaction:

5,10-methylenetetrahydrofolate + glycine + H_2O = tetrahydrofolate + L-serine.

It is a pyridoxal phosphate-requiring enzyme that interconverts glycine and serine; it transfers a hydroxymethyl group from N^5,N^{10}-methylenetetrahydrofolate to a glycine-pyridoxal phosphate Schiff base or from a serine-pyridoxal phosphate Schiff base to tetrahydrofolate. Example, cytosolic enzyme from *Neurospora crassa*: database code GLY1_NEUCR, 479 amino acids (52.76 kDa).

glycine receptor a complex of integral membrane proteins that binds glycine and mediates its effects as an inhibitory neurotransmitter in lower brain areas and spinal cord. The receptor is a pentamer of α (four isoforms, α1–α4) and β subunits. The receptor forms an intrinsic Cl^- channel, blocked by strychnine (distinguishing it from the $GABA_A$ Cl^- channel). All subunits have four transmembrane segments, M1–M4, M3 and M4 being separated by a cytoplasmic hydrophilic loop; this is comparable to nicotinic acetylcholine receptors (*see* **cholinoceptor**) and $GABA_A$ receptors (*see* **GABA receptor**), with which some sequence similarities also exist. Glycine also binds to a site on the NMDA (glutamate) receptor, which must be occupied by glycine to enable activation of the receptor by NMDA, and is also blocked by strychnine. Examples (all precursors) from *Rattus norvegicus*: α1, database code GRA1_RAT, 449 amino acids (51.68 kDa); α2, database code GRA2_RAT, 452 amino acids (52.05 kDa); α3, database code GRA3_RAT, 464 amino acids (53.67 kDa); β, database code GRB_RAT, 496 amino acids (55.93 kDa).

glycinin a 350 kDa **globulin** that is the chief protein constituent of the soya bean, *Glycine max*. It resembles **arachin**, **edestin**, and **excelsin** structurally.

glycinium glycine cation; the cation, H_3N^+–CH_2–COOH, derived from **glycine**.

glycino the alkylamino group, HOOC–CH_2–NH–, derived from **glycine**.

glycitol *an obsolescent name for* **alditol**.

glyco+ *or (before a vowel)* **glyc+** *comb. form* **1** indicating sweet-tasting. **2 a** indicating sugar. **b** (*in medicine*) indicating glucose. *See also* **gluco+**. **3** *(in chemical nomenclature)* indicating covalently linked to carbohydrate. **4** indicating combination with glycine; e.g. **glycocholate**, **glycocyamine**.

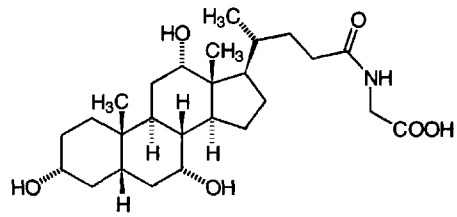
glycoamino acid any compound in which a saccharide is combined with an amino acid through any kind of covalent linkage. The term includes **glycosylamino acids**.

glycobiology the branch of biochemistry dealing with **glycoconjugates**, including their structure, analysis, function, and metabolism.

glycocalicin a carbohydrate-rich hydrophilic fragment, M_r 130 000, cleaved from the external portion of the α chain of **glycoprotein Ib** by protease action.

glycocalyx *or* **cell coat** a zone surrounding many plant and animal cells that is rich in glycoproteins and proteoglycans.

glycocholate **1** the anion of glycocholic acid; *N*-cholylglycine; a bile acid. The anions of similar glycine conjugates of other bile acids are known, e.g. glycochenodeoxycholate, **glycodeoxycholate**, glycolithocholate. **2** any salt of glycocholic acid. Sodium glycocholate is the chief **bile salt** in humans and herbivorous animals. It is useful as a detergent; aggregation number 2.1, CMC 7.1 mM.



glycocholic acid

glycocoll *an obsolete name for* **glycine**.

glycoconjugate *or (formerly)* **glucoconjugate** any large and complex biological molecule that contains a carbohydrate moiety. The term comprehends glycolipid, glycopeptide, glycoprotein, peptide glycan, proteoglycan, and heteroglycan. *See also* **glyco+** (def. 3), **conjugate** (def. 5).

glycocyamine *an older name for N*-amidinoglycine; guanidinoacetic acid. In polychaete worms, the guanidine group can undergo phosphorylation to phosphoglycocyamine, which acts as a **phosphagen**.

glycodeoxycholate **1** glycodeoxycholic acid; *N*-deoxycholylglycine; a bile acid. **2** any salt of glycodeoxycholic acid; sodium glycodeoxycholate is useful as a detergent; aggregation number 2, CMC 2.1 mM.

glycoform any of several differently glycosylated variants of a specified glycoprotein. Glycoforms may vary in the type, number, and/or position of the sugar residues, differ in their physiological properties (e.g. rate of action), and occur together in a given tissue.

glycogen a polydisperse, highly branched glucan or polyglucose, composed of chains of D-glucose residues in $\alpha(1\rightarrow4)$ glycosidic linkage, joined together by $\alpha(1\rightarrow6)$ glycosidic linkages; a small number of $\alpha(1\rightarrow3)$ glycosidic linkages and some cumulative $\alpha(1\rightarrow6)$ links also may occur. Its structure is similar to that of **amylopectin** but with more, though rather shorter, branches; those in glycogen variously contain 8 to 12 glucose residues. The size of the molecule varies greatly according to source and method of measurement, with average M_r values of 2.5×10^5 to upwards of 1.5×10^7 reported. Glycogen serves as a cellular store of glucose; it occurs, frequently as granules, in all animal tissues, especially liver and skeletal muscle, and also in some bacteria and yeasts. The glycogen molecule is linked to the protein **glycogenin** which is required for the *ab initio* synthesis of glycogen by **glycogen synthase**.

glycogenase *an alternative name for* either **α-amylase** or **β-amylase**.

glycogen branching enzyme *see* **branching enzyme**.

glycogen disease *or* **glycogen storage disease** *or* **glycogenosis** any human disease in which there is an inherited abnormality in glycogen metabolism. Such diseases have been classified into eight types. Type I glycogen disease (*or* **von Gierke's disease**) involves a deficiency of hepatic **glucose-6-phosphatase**. It is an inherited autosomal recessive disease of infants, characterized by massive hepatomegaly, failure to thrive, severe hypoglycemia, and increased hepatic content of normal glycogen. Type II glycogen disease (*or* **Pompe's disease**) involves a generalized deficiency of lysosomal **α-glucosidase**. It is an inherited autosomal recessive disease of infants, characterized by massive cardiomegaly, hypotonia, and an increased content of normal glycogen in virtually all tissues. Type III glycogen disease (*or* **limit dextrinosis** *or* **Cori's disease**) involves a generalized deficiency of amylo-1,6-glucosidase (debrancher enzyme) (EC 3.2.1.33). It is an inherited autosomal recessive disease of infants that is similar to, but milder than, type I glycogen disease. It is characterized by an elevated content of glycogen in muscle, liver, and erythrocytes, the glycogen having abnormally short outer branches. A number of subtypes

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have been recognized. Type IV glycogen disease (*or* **amylopectinosis** *or* **Andersen's disease**) is a rare condition of infants in which there is a generalized deficiency of 1,4-α-glucan branching enzyme (EC 2.4.1.18). It is characterized by hepatic cirrhosis, hepatosplenomegaly, ascites, and glycogen with abnormally long outer branches; the glycogen may not accumulate excessively. Type V glycogen disease (*or* **McArdle's disease**) involves a deficiency of glycogen phosphorylase (EC 2.4.1.1) in voluntary muscle. The disease is probably inherited as an autosomal recessive. It is characterized by myoglobinuria and painful cramps occurring during strenuous exercise, symptoms that do not usually appear until 20 years of age. There is no hypoglycemia but muscular exercise fails to elevate the blood lactate concentration. Type VI glycogen disease (*or* **Hers's disease**) involves an increased hepatic glycogen content and a lowered hepatic glycogen phosphorylase (EC 2.4.1.1) activity but a normal phosphorylase-activating system. The clinical course is mild. Type VII glycogen disease involves a deficiency of muscle 6-**phosphofructokinase**. The disease is probably inherited as an autosomal recessive and is clinically identical to Type V glycogen disease. There are raised contents in muscles of normal glycogen, glucose 6-phosphate, and fructose 6-phosphate, together with a lower than normal concentration of fructose 1,6-bisphosphate. Type VIII glycogen disease involves a reduced **phosphorylase kinase** activity in the liver and in leukocytes. Thought to be inherited as an X-linked character, the disease is characterized by mild hepatomegaly, increased liver glycogen content, and mild hypoglycemia.

glycogenesis *a former term for* **1 glyconeogenesis. 2 gluconeogenesis. 3 glucogenesis. 4** the metabolic formation of glycogen from sugar (i.e. glucose).

glycogenetic of or relating to the production of glycogen. (*Note*: The term is often used confusingly in the senses of **glycogenic** (def. 1, 2).)

glycogenic 1 of, relating to, or involving glycogen. **2** of or relating to the formation of sugar (i.e. glucose), especially in animals; glucogenic. (*Note*: the term is often used confusingly in the sense of **glycogenetic**.)

glycogenin EC 2.4.1.186; *recommended name*: glycogenin glucosyltransferase; a protein that is required for the initiation of glycogen synthesis by glycogen synthase. Glycogenin catalyses formation of a glycosidic link between a glucose and one of its own tyrosines (Tyr^{194} in human) and then catalyses addition of a further five glucose molecules. UDPglucose is the donor of the glucose units. This forms a primer which is then extended with further glucose molecules by **glycogen synthase**. Glycogen synthase is only catalytically efficient when it is bound to glycogenin. This has two consequences: first, the number of glycogen granules is determined by the number of molecules of glycogenin, and second, elongation stops when the synthase is sterically prevented from contact with glycogenin, which forms the core of the particle. Hence, the glycogenin–synthase interaction limits the size of glycogen granules. Glycogenin is a monomeric glycoprotein (via its reactivity), tightly bound to the 86 kDa catalytic subunit of glycogen synthase. Example from *Oryctolagus cuniculus*: database code GLYG_RABIT, 332 amino acids (37.27 kDa).

glycogenolysis the breakdown of glycogen into glucose, either by hydrolysis or via glucose 1-phosphate and glucose 6-phosphate. The term is sometimes restricted to the phosphorolysis of glycogen to glucose 1-phosphate. —**glycogenolytic** *adj.*

glycogenosis *an alternative name for* **glycogen disease**.

glycogen phosphorylase *see* **phosphorylase**.

glycogen storage disease *an alternative term for* **glycogen disease**.

glycogen synthase EC 2.4.1.11; *recommended name* (example): glycogen (starch) synthase (the nature of the synthetic product should be included in the name); *systematic name*: UDPglucose:glycogen 4-α-D-glucosyltransferase; *other name*: UDPglucose–glycogen glucosyltransferase. An enzyme that catalyses the reaction between UDPglucose and (1,4-α-D-glucosyl)$_n$ to form (1,4-α-D-glucosyl)$_{n+1}$ with release of UDP. The mammalian enzyme requires glucosylated **glycogenin** as a primer (product of glycogenin glucosyltransferase, EC 2.4.1.186), and is susceptible to allosteric activation by glucose 6-phosphate, and phosphorylation by a cyclic AMP-dependent kinase. Example from human muscle: database code UGST_HUMAN, 737 amino acids (83.77 kDa). *See also* **dependent form of glycogen synthase, glycogenin, starch synthase**.

[glycogen-synthase-D] phosphatase EC 3.1.3.42; an enzyme that hydrolyses phosphate from glycogen synthase D, thereby activating it.

glycoglycerolipid any **glycolipid** containing one or more glycerol residues.

glycohemoglobin *or (esp. UK)* **glycohaemoglobin** *an alternative term for* **glycated hemoglobin**.

glycoinositolphospholipid *see* **GPI anchor**.

glycol 1 ethylene glycol; ethane-1,2-diol; $HOCH_2–CH_2OH$. **2** *or* **glychol** any dihydric alcohol, i.e. any compound in which two alcoholic hydroxyl groups are on different carbon atoms (which are usually but not necessarily adjacent).

glycolaldehyde hydroxyacetaldehyde; hydroxyethanal; $HOCH_2–CHO$.

glycolate *or (formerly)* **glycollate 1** *the trivial name for* hydroxyacetate; hydroxyethanoate; the anion, $HOCH_2–COO^-$, derived from **glycolic acid**. It is an important metabolite in C_3 plants. **2** any mixture of glycolic acid and its anion. **3** any salt or ester of glycolic acid. It is formed from phosphoglycolate, a product of **ribulose bisphosphate carboxylase** when this is acting as an oxidase. It is converted to glyoxylate by glycolate oxidase (*see* **2-hydroxy-acid oxidase**).

glycolate oxidase an FMN-containing enzyme that oxidizes glycolate to glyoxylate in plant peroxisomes. It is now included with **2-hydroxy-acid oxidase**.

glycolic acid *or (formerly)* **glycollic acid** hydroxyacetic acid; hydroxyethanoic acid; $HOCH_2–COOH$; a constituent of sugar-cane juice.

glycolipid any compound containing (usually) one to four linked glycose (monosaccharide) residues joined by a glycosyl linkage to a lipid moiety (e.g. to a mono- or diacylglycerol, to a long-chain base such as sphingosine, or to a ceramide) or (in a bacterial glycolipid) joined in ester linkage to one or more fatty-acid molecules. The term embraces **galactolipid**. *See also* **cerebroside, ganglioside, lipopolysaccharide**.

glycollate *an obsolete variant spelling of* **glycolate**.

glycoloyl *symbol*: Gc; the acyl group, $HOCH_2–CO–$, derived from **glycolic acid**.

glycolytic pathway *or* **Embden–Meyerhof(–Parnas) pathway** the widely distributed, extra-mitochondrial, cellular metabolic pathway by which sugars, sugar phosphates, or their precursors are broken down with an overall negative free energy change favourable to formation of ATP; the pathway yields usually pyruvate aerobically or lactate anaerobically in animal tissues. By extension, the term is also used of similar processes in other organisms yielding, sometimes, other products, e.g. ethanol, glycerol, etc. Overall there is a net yield of 2 ATP for each glucose metabolized, since phosphorylation of the hexose substrates requires 2 ATP, but conversion to pyruvate of the two 3-carbon substrates formed yields 2 ATP for each. The pathway from glucose involves its conversion to glucose 6-phosphate, thence successively to fructose 6-phosphate, fructose 1,6-bisphosphate, glyceraldehyde 3-phosphate plus glycerone phosphate (which is converted to glyceraldehyde 3-phosphate in situations in which it is further degraded), 1,3-bisphosphoglycerate, 3-phosphoglycerate, 2-phosphoglycerate, phospho*enol*pyruvate, and pyruvate. The enzymes involved are hexokinase, glucose-6-phosphate isomerase, phosphofructokinase, fructose-bisphosphate aldolase, triose-phosphate isomerase, glyceraldehyde-3-phosphate dehydrogenase, phosphoglycerate kinase, phosphoglycerate mutase, enolase, and pyruvate kinase (*see* individual entry for each enzyme). Glyco-

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gen breakdown (**glycogenolysis**) by phosphorylase yields glucose 1-phosphate, which is converted by phosphoglucomutase to glucose 6-phosphate, which in muscle is then degraded by the pathway outlined above. The pathway is subject to hormonal regulation, especially by insulin, glucagon, and epinephrine. Flux through the pathway is under powerful regulation by phosphofructokinase, the main modulator of which is **fructose 2,6-bisphosphate**.

glycolytic oscillator any metabolic activity that produces periodic regular oscillations in the concentrations of intermediates of the **glycolytic pathway**. Such oscillations have been observed in glycolysing yeast cells and extracts of skeletal muscle and heart. These oscillations reflect periodic changes in the activity of **phosphofructokinase** in response to changes in the levels of its activators and inhibitors in the system being studied.

glycon *or (formerly)* **glycone** the carbohydrate moiety of any **glycoside** that also contains a noncarbohydrate component.

glyconeogenesis **1** *an alternative name for* **gluconeogenesis**. **2** *(sometimes)* the formation of glycogen from noncarbohydrate precursors.

glyconic acid *an obsolescent name for* **aldonic acid**.

glycopeptide any compound in which carbohydrate is covalently attached to an oligopeptide composed of residues of L- and/or D-amino acids. The term usually denotes a product of proteolytic degradation of a glycoprotein but includes glycated peptide. It should be distinguished from **peptidoglycan**, for which it is sometimes considered to be a synonym.

glycophorin any of several type I membrane proteins of the erythrocyte membrane. They are carbohydrate-rich sialoglycoproteins (SGPs – hence the nomenclature for glycophorins: αSGP, etc.), and stain with periodic acid–Schiff (PAS) reagent (hence the nomenclature PAS 1, etc. for bands on electrophoresis). The glycosylated moiety serves as an antigenic determinant and as a receptor for viruses and plant agglutinins. A glycophorin was the first membrane protein to have its full sequence elucidated. There is a single membrane-spanning domain. **Glycophorin A** (*or* αSGP) is the major sialoglycoprotein of the human erythrocyte membrane. On electrophoresis it occurs in PAS 1 (dimer). It has a molecular mass of ≈31 kDa, contains 60% carbohydrate by weight, and consists of a 131-residue polypeptide chain that spans the cell membrane; all the carbohydrate is attached to the N-terminal half and is exposed to the exterior of the cell. Glycophorin A displays either M or N blood group activity (*see* **MNSs system**), depending on which of two alternative pairs of amino-acid residues occurs at positions 1 and 5 in the sequence. It binds influenza virus. Database code (precursor) GLPA_HUMAN, 150 amino acids (16.25 kDa). **Glycophorin B** (*or* δSGP), also from the human erythrocyte membrane, is a minor sialoglycoprotein similar to glycophorins A and E. It occurs in PAS 3 and has an amino-acid sequence identical in its N-terminal segment with that of glycophorin A_N. It carries the immunodeterminants for the N and Ss antigens (*see* **MNSs system**). Database code (precursor) GLPB_HUMAN, 91 amino acids (9.78 kDa). **Glycophorin C** (*or* βSGP) occurs in PAS 2, glycoconnectin; it is a minor sialoglycoprotein that probably contains blood group Gerbich antigens and receptors for *Plasmodium falciparum* (malaria) merozoites. Database code (precursor) GLPC_HUMAN, 128 amino acids (13.80 kDa). **Glycophorin E** is similar to glycophorins A and B. Database code GLPE_HUMAN, 78 amino acids (8.52 kDa).

glycoprotein any protein that contains covalently bound glycose (i.e. monosaccharide) residues other than as a moiety of nucleic acid; the glycose occurs most commonly as oligosaccharide or fairly small polysaccharide but occasionally as monosaccharide. Glycoproteins are widespread in animals and in the primary cell walls of plants. The term includes glycated protein and is now considered also to include **proteoglycan**. *Compare* **mucoprotein**.

glycoprotein hormone *general name for* any member of a family of closely related mammalian hormones of the pituitary and placenta, believed to be derived by biochemical evolution from a common primitive molecule. The group comprises the three gonadotropins, namely pituitary **follicle-stimulating hormone**, pituitary **LH**, and placental **chorionic gonadotropin**, plus pituitary **thyrotropin**; all have two peptide chains, α and β, each with attached, variable carbohydrate substituent groups that account for 15–31% of the molecular mass. In any given species, the amino-acid sequences of the α chains are identical, or nearly so, in all these hormones, whereas the β chains have greater differences in amino-acid sequence and confer hormonal specificity on the molecules.

glycoprotein Ib *abbr.*: GP-Ib; a surface membrane protein of platelets that participates in the formation of platelet plugs by binding to von Willebrand factor. It is a disulfide-linked heterodimer of α and β subunits. Examples (precursors) from human: α subunit, database code GPBA_HUMAN, 626 amino acids (68.88 kDa); β subunit, database code GPBB_HUMAN, 206 amino acids (21.69 kDa).

glycoprotein *N*-palmitoyltransferase EC 2.3.1.96; an enzyme that catalyses a reaction between palmitoyl-CoA and a glycoprotein to give *N*-palmitoylglycoprotein with release of CoA.

glycosaemia *a variant spelling (esp. Brit) of* glycosemia (*see* **glycemia**).

glycosamine *an older name for* **aminodeoxysugar**, now restricted to some trivial names. *Distinguish from* **glycosylamine**.

glycosaminoglycan any glycan (i.e. polysaccharide) containing a substantial proportion of aminomonosaccharide residues.

glycosaminopeptide *(sometimes) an alternative name for* **peptidoglycan**.

glycosan *an old term (not recommended) for* any anhydrosugar whose formation involves its reducing group. *Distinguish from* **glycan**.

glycose **1** *a less frequently used term for* any monosaccharide. **2** *an obsolete name for* **glucose** (*see also* **glyco+** (def. 2)). **3** *(sometimes) an alternative name for* **corn syrup**.

glycosemia *or (esp. Brit)* **glycosaemia** *an alternative name for* **glycemia**.

glycosidase any hydrolase of subclass EC 3.2, enzymes that hydrolyse glycosidic linkages. Glycosidases are subdivided into those that hydrolyse *O*-glycosyl compounds (EC 3.2.1), *N*-glycosyl compounds (EC 3.2.2), or *S*-glycosyl compounds (EC 3.2.3). Some glycosidases can also transfer glycosyl residues to oligosaccharides, polysaccharides, or other acceptor alcohols. *See also* **(DNA) glycosylase**, **glucosidase**.

glycoside *or* **oside** **1** any compound in which a **glycosyl** group is substituted into a hydroxyl group, a thiol group, or a selenol group in another compound; such a substance may be named, respectively, *O*-glycoside, *S*-glycoside (or thioglycoside), or *Se*-glycoside (or selenoglycoside). A glycoside is either a mixed acetal (if derived from a cyclic form of an aldose) or a mixed ketal (if derived from a cyclic form of a ketose). By extension, any compound formed by attachment of a glycosyl group to a hydrocarbyl group has been termed a *C*-glycoside and that by attachment of a glycosyl group to an amino or substituted amino group has been termed also *N*-glycoside (or nitrogen glycoside), but these terms are misnomers and should not be used; the preferred terms are ***C*-glycosyl compound** and **glycosylamine**, respectively. *See also* **cardiac glycoside**, **nucleoside**. **2** *an obsolete term for* **glucoside**.

glycosidic **1** of, pertaining to, or being a **glycoside**. **2** *an alternative term for* **anomeric** (def. 2).

glycosidic bond the covalent bond between the anomeric carbon atom of a saccharide and some other group or molecule with which it forms a glycoside.

glycosiduronate **1** the anion of a **glycosiduronic acid**. **2** any salt or ester of a glycuronic acid.

glycosiduronic acid *or (formerly)* **glycuronide** a glycoside of any **uronic acid**.

glycosome a microbody-like organelle present in *Trypano-*

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soma brucei and containing nine enzymes involved in glycolysis, and glycerol kinase.

glycosphingolipid any compound containing residues of a sphingoid and at least one monosaccharide. Glycosphingolipids are subdivided into: (1) neutral glycosphingolipids, comprising monoglycosyl- and oligoglycosylsphingoids and monoglycosyl- and oligoglycosylceramides; and (2) acidic glycosphingolipids, comprising sialosylglycosylsphingolipids (**gangliosides**) and sulfoglycosylsphingolipids (formerly known as sulfatides).

glycostatic maintaining a constant level of sugar, e.g. of glucose or glycogen. *Compare* **glycotropic**.

glycosuria the presence of abnormally high concentrations of glucose and/or other sugars in the urine. *See also* **glucosuria**, **fructosuria**.

glycosyl any chemical group formed by detaching the anomeric, i.e. glycosidic, hydroxyl group from the cyclic form of a monosaccharide or monosaccharide derivative, or (by extension) of a lower oligosaccharide or oligosaccharide derivative.

glycosylamine any compound formed by the replacement of the anomeric, i.e. glycosidic, hydroxyl group of a cyclic form of a monosaccharide or monosaccharide derivative by an amino group or a substituted amino group. (The term **nitrogen glycoside** (*or* ***N*-glycoside**) is a misnomer for glycosylamine and should not be used.) *Distinguish from* **glycosamine**.

glycosylamino acid any **glycoamino acid** in which the saccharide moiety is in glycosyl (*O*-, *N*-, or *S*-) linkage to the amino-acid moiety. These are obtained by enzymic or chemical cleavage of glycoproteins or by chemical or enzymic synthesis.

glycosylase *see* **(DNA) glycosylase**.

glycosylasparaginase *see* **N^4-(β-*N*-acetylglucosaminyl)-L-asparaginase**.

glycosylated hemoglobin *a misnomer for* **glycated hemoglobin**.

glycosylation substitution of one or more **glycosyl** groups into a chemical compound or group. —**glycosylated** *adj.* *See also* **glycation**.

***C*-glycosyl compound** any compound formed by the replacement of the anomeric, i.e. glycosidic, hydroxyl group of a cyclic form of a monosaccharide or monosaccharide derivative by an organyl group. The term ***C*-glycoside** is a misnomer for *C*-glycosyl compound and should not be used.

glycosyloxy any chemical group formed by detaching the hydrogen atom from the anomeric, i.e. glycosidic, hydroxyl group of the cyclic form of a monosaccharide or monosaccharide derivative.

glycosylphosphatidylinositol *see* **GPI anchor**.

glycosyltransferase any enzyme transferring a glycosyl group. Glycosyltransferases belong to subclass EC 2.4, which includes hexosyltransferases (EC 2.4.1.1 to 2.4.1.206); pentosyltransferases (EC 2.4.2.1 to 2.4.2.37); and enzymes transferring other glycosyl groups (EC 2.4.99.1 to 2.4.99.11).

glycotropic increasing the concentration of glucose in the blood. *Compare* **glycostatic**.

glycuronan *or (formerly)* **polyuronide** any glycan composed entirely of uronic-acid residues.

glycuronic acid *an obsolete term for* **uronic acid**.

glycuronide *the former term for* **glycosiduronic acid**.

glycyl the acyl group, NH_2–CH_2–CO–, derived from **glycine**.

glycyl chain *a name sometimes applied to* the **A chain** of any of those species of insulin whose amino-acid sequences were the first to be determined. It is so-called by virtue of the N-terminal glycine residue occurring in those instances.

glycylglycine a dipeptide useful for the preparation of buffers in the pH range around its pK_a (20 °C) of 8.40.

glycyrrhiza *also called* **liquorice** *or (esp. US)* **licorice**; a preparation obtained from the dried roots of the leguminous shrub, *Glycyrrhiza glabra*, with flavouring and medical uses.

glycyrrhizic acid 20β-carboxy-11-oxo-30-norolean-12-en-3β-yl-2-*O*-β-D-glucopyranuronosyl-α-D-glucopyranosiduronic acid; a glycosiduronic acid extracted from *Glycyrrhiza (see* **glycyrrhiza**); it has an intensely sweet taste.

glyoxal ethanedial; OHC–CHO; the dialdehyde analogue of glycol and oxalic acid.

glyoxalase I EC 4.4.1.5; *recommended name*: lactoylglutathione lyase, *other name*: methylglyoxalase. An enzyme catalysing the reaction:

(*R*)-*S*-D-lactoylglutathione = glutathione + methylglyoxal.

glyoxalase II EC 3.1.2.6; *recommended name*: hydroxyacylglutathione hydrolase. An enzyme catalysing the reaction:

S-(2-hydroxyacyl)glutathione + H_2O = glutathione + a 2-hydroxy-acid anion.

glyoxalate *a former name for* **glyoxylate**.

glyoxaline *an alternative name for* **imidazole**.

glyoxylate *or (formerly)* **glyoxalate** **1** the anion, OHC–COO^-, derived from glyoxylic acid. **2** any salt or ester of glyoxylic acid.

glyoxylate cycle *or* **glyoxylate pathway** a modification of the **tricarboxylic-acid cycle** occurring in some plants and microorganisms, in which isocitrate, instead of being dehydrogenated, is cleaved as described under **isocitrate lyase** to glyoxylate and succinate. This serves to generate glyoxylate from the acetyl moiety of acetyl-CoA. The glyoxylate can then react with another molecule of acetyl-CoA to form malate, a reaction catalysed by **malate synthase**. These two reactions taken together allow a four-carbon molecule, malate, and hence carbohydrate, to be formed from acetyl-CoA, which, in turn, may be formed from fatty acids. In some plants the enzymes of the glyoxylate pathway are present in **glyoxysomes**.

glyoxysome a cellular organelle, of density 1.25 g cm^{-3}, found in the organs of fatty seedlings where fat is being converted to carbohydrate. It contains the enzymes of the **glyoxylate cycle** and most of the particulate beta-oxidation activity.

glyphosate *N*-(phosphonomethyl)glycine; a potent, systemically acting, nonselective herbicide, present as its isopropylamine salt in some commercial weedkillers. It functions by inhibiting 5-*enol*pyruvylshikimate-3-phosphate (EPSP) synthase. *See also* **shikimate**. *Proprietary names* include Roundup and Tumbleweed.

glypiation the attachment or process of attachment of glycosylphosphatidylinositol to proteins. *See* **GPI anchor**.

GM *or* **G-M** *abbr. for* Geiger–Müller (e.g. in **GM counter** for Geiger–Müller counter).

GM-CSF *abbr. for* granulocyte/macrophage colony stimulating factor. *See* **colony stimulating factor**.

GMD *(in clinical chemistry) abbr. for* **glutamate dehydrogenase (NAD(P)$^+$)**.

GMP *abbr. for* guanosine monophosphate i.e. guanosine phosphate.

GMP synthase EC 6.3.5.2; *recommended name*: GMP synthase (glutamine-hydrolysing); *systematic name*: xanthosine-5-phosphate:L-glutamine amido-ligase (AMP-forming); *other names*: GMP synthetase (glutamine-hydrolysing); glutamine amidotransferase. An enzyme that catalyses a reaction between ATP, xanthosine 5′-phosphate, L-glutamine, and H_2O to form AMP, pyrophosphate, guanosine monophosphate, and L-glutamate. It is inhibited by azaserine and 6-diazo-5-oxonorleucine, in common with other glutamine amidotransferases. It has four motifs and a region conserved in amidotransferases (one motif). Example from *Escherichia coli*: database code GUAA_ECOLI, 525 amino acids (58.61 kDa).

GMT *(in clinical chemistry) abbr. for* **glutamyltransferase**.

gnotobiotic describing an organism, especially a higher animal, or its environment, that has been deliberately rendered free of microorganisms and other organisms, including parasites, commensals, and symbionts, that it would normally harbour, or that harbours only a few, known, such organisms.

GnRH *abbr. for* gonadotropin-releasing hormone.

GNTR a transcriptional repressor for the gluconate (*gnt*) operon in *Bacillus subtilis*. The *gnt* operon is induced by gluconic acid δ-lactone; this was the first of a family of *gnt* re-

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pressors with **helix-turn-helix** motifs. Database code GNTR_BACSU, 243 amino acids (28.25 kDa).

goblin a protein of avian erythrocyte plasma membranes and M_r 260 000. It undergoes phosphorylation, and is highly homologous with **ankyrin**, of which it is the avian equivalent.

GOD *(sometimes) abbr. for* glucose oxidase.

godnose a name proposed for ascorbic acid by A. Szent-Györgyi, as an alternative to **ignose**, before he knew its structure.

GOGAT *abbr. for* glutamine (amide):2-oxoglutarate aminotransferase (oxidoreductase NADP$^+$). It is now known to be two enzymes, renamed **glutamate synthase (ferredoxin)** and **glutamate–ammonia ligase**.

goitre *or (US)* **goiter** any swelling of the thyroid gland. Although common in areas where dietary iodine is insufficient, the condition is not related to thyroid state and patients with goitre may be euthyroid, hyperthyroid, or hypothyroid.

goitrogen any agent or factor causing goitre.

Goldstein, Joseph Leonard (1940–), US physician and molecular geneticist notable for his discovery (in collaboration with M. S. **Brown**) of cellular receptors for low-density lipoproteins and their role in the removal of cholesterol from the bloodstream; Nobel Laureate in Physiology or Medicine (1985) jointly with M. S. Brown 'for their discoveries concerning the regulation of cholesterol metabolism'.

Golgi, Camillo (1843–1926), Italian anatomist, cytologist, neurologist, and pathologist remembered for his cytological studies of the central nervous system, for the introduction of techniques for staining cells with metallic salts, and in particular for his discovery thereby of the cellular organelle named after him (*see* **Golgi apparatus**); Nobel Laureate in Physiology or Medicine (1906) jointly with S. Ramón y Cajal 'in recognition of their work on the structure of the nervous system'.

Golgi apparatus *or* **Golgi body** *or* **Golgi complex** a compound membranous cytoplasmic organelle of eukaryotic cells, consisting of flattened, ribosome-free vesicles arranged in a more or less regular stack. The Golgi apparatus differs from the endoplasmic reticulum in often having slightly thicker membranes, appearing in sections as a characteristic shallow semicircle so that the convex side (*cis* or entry face) abuts the endoplasmic reticulum, secretory granules emerging from the concave side (*trans* or exit face). In vertebrate cells there is usually one such organelle, while in invertebrates and plants, where they are known usually as **dictyosomes**, there may be several scattered in the cytoplasm. The Golgi apparatus processes proteins produced on the ribosomes of the rough endoplasmic reticulum; such processing includes modification of the core oligosaccharides of glycoproteins, and the sorting and packaging of proteins for transport to a variety of cellular locations, e.g. to storage granules, lysosomes, or secretory vesicles. The Golgi is a major site of synthesis of polysaccharides, including the **pectin** and hemicellulose of the plant cell wall and most of the glycosaminoglycans of the extracellular matrix in animals. Three different regions of the Golgi are now recognized both in terms of structure and function: *cis*, in the vicinity of the *cis* face, *trans*, in the vicinity of the *trans* face, and *medial*, lying between the *cis* and *trans* regions. While the **luminal proteins** of the endoplasmic reticulum leave it together with the proteins to be secreted, they are retrieved from the *cis* network and returned to the endoplasmic reticulum. Thus transport occurs in both directions. The drug **brefeldin A** blocks protein secretion through the Golgi but does not appear to block the return pathway. **Galactosyltransferase** is a marker enzyme for the *trans* membranes while ***N*-acetylglucosaminyltransferase** III serves this role for the medial membranes. [After Camillo **Golgi**, who, in 1898, was the first to describe it.]

Golgi mannosidase EC 3.2.1.114; *recommended name*: mannosyl-oligosaccharide 1,3-1,6-α-mannosidase; *systematic name*: 1,3-(1,6-)mannosyl-oligosaccharide α-D-mannohydrolase; *other name*: mannosidase II. An enzyme that catalyses the hydrolysis of the terminal 1,3- and 1,6-linked α-D-mannose residues in the mannosyl-oligosaccharide $Man_5GlcNAc_3$. It is a type II membrane protein, and a glycosyl hydrolase enzyme in all tissues, mostly in adrenal and thymus. It belongs to a family of glycosyl hydrolases. Example from mouse: database code MAN2_MOUSE, 1150 amino acids (131.44 kDa).

golgiosome *an alternative name for* **dictyosome**.

gonad any animal organ that produces gametes. In some species the gonads also produce hormones. —**gonadal** *adj.*

gonadoliberin *recommended name for* **gonadotropin-releasing hormone**.

gonadotropic hormone *or* **gonadotrophic hormone** *a former name for* **gonadotropin**.

gonadotropin *or (formerly)* **gonadotrophin** *or* **gonadotropic hormone** *or* **gonadotrophic hormone** **1** any mammalian glycoprotein hormone that stimulates gonadal function. Strictly, gonadotropins comprise the adenohypophyseal hormones **follicle-stimulating hormone** (FSH) and **luteinizing hormone** (LH) together with the placental hormone **choriogonadotropin**, but the term is often extended to include also the adenohypophyseal hormone **prolactin** (which is not a glycoprotein but has gonadotropic activity). **2** any single substance having the combined activities of FSH and LH, such as choriogonadotropin or the gonadotropic hormones of cold-blooded vertebrates. **3** any impure hormonal preparation displaying the separate activities of FSH and LH, such as (human) menopausal gonadotropin (i.e. urogonadotropin) and **pregnant mare's serum gonadotropin**. —**gonadotropic** *adj.*

gonadotropin-releasing factor *abbr.*: GnRF; *another name for* **gonadotropin-releasing hormone**.

gonadotropin-releasing hormone (*abbr.*: GnRH) *or* **gonadoliberin** (recommended name) *or* **luteinizing hormone/follicle-stimulating hormone releasing factor** (*abbr.*: LH/FSH-RF) a family of decapeptide amides, of which there are at least seven members. They have been found in many vertebrate species from jawless fish (lamprey) to higher mammals. The structure is highly conserved; the sequence Glp-His-Trp-Ser-Tyr-Gly-Leu-Arg-Pro-Gly-NH_2 is common to all mammals; among other species, position 8 is most variable, positions 1, 2, 4, 9, and 10 being invariant. It is named after its function in mammals, in which it is released by the hypothalamus into the hypophyseal portal circulation in response to neural and/or chemical stimuli, and is considered to be the sole neuropeptide causing the release of FSH and LH by the anterior pituitary. In mammals it is also expressed in the placenta, and its functions across phylogenetic classes may include actions as a neurotransmitter, neuromodulator or local hormone. It is synthesized as a much larger precursor, example from rat: database code GONL_RAT, 93 amino acids (10.5 kDa); residues 1–23 are the signal peptide, 24–33 GnRH (35 and 36 are a dibasic cleavage site, Gly^{34} provides the amide group) and 37–92 are a peptide (GnRH-associated peptide, *abbr.*: GAP) initially thought to inhibit secretion of prolactin-releasing hormone, but its role is not well understood and it is poorly conserved.

gonadotropin-releasing hormone receptor *abbr.*: GnRHR; any of a family of integral membrane proteins that bind GnRH and mediate its intracellular effects. They are found not only in pituitary, but also in ovary, testis, breast, and prostate. These are seven-transmembrane-helix G-protein-coupled receptors, that stimulate the phosphatidylinositol-Ca^{2+} second messenger system. Example from *Rattus norvegicus*: database code GRHR_RAT, 327 amino acids (37.75 kDa).

gonane the parent 17-carbon tetracyclic hydrocarbon of steroids and bile acids.

gondoic acid *see* **eicosenoic acid**.

gonosome any motile animal germ cell, e.g. a spermatozoon.

Good buffer substance *or* **Good's buffer (substance)** any member of a collection of **zwitterionic buffer** substances selected or devised for suitability in experimental biological systems according to a number of predetermined criteria. These in-

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clude: ease of preparation and purification; high solubility in water; low temperature coefficient of pK_a; and high transparency to light or ultraviolet light of wavelengths greater than 230 nm. The original lists included substances having the following trivial names (pK_a values at 20 °C are in parentheses): **Mes** (6.15), **Ada** (6.6), **Pipes** (6.8), **Aces** (6.9), **Bes** (7.15), **Mops** (7.2), **Tes** (7.5), **Hepes** (7.55), **Hepps** (8.0), **Tricine** (8.15), **Bicine** (8.35), and **Taps** (8.4); **Ches** (9.3 at 25 °C) and **Caps** (10.4) have similar properties. [After Norman Everett Good (1917–), US plant pathologist.]

gossypol a pigment found in cottonseed and containing two naphthalene rings with multiple –OH and other groups. It has antispermatogenic activity, and has been used (in China) as a male contraceptive. It is a potent inhibitor of contractions of strips of guinea-pig lung induced by platelet-activating factor or leukotriene, and it inhibits 5- and 12-lipoxygenase.

GOT *(in clinical chemistry) abbr. for* glutamate-oxaloacetate transaminase (AST preferred). *See* **transaminase**.

gout a condition characterized by inflammation of the joints and cartilage due to hyperuricemia and consequent deposition of monosodium urate crystals in the joints, often within polymorphonuclear leukocytes. The hyperuricemia results from overproduction of uric acid, which may be due to elevated activity of ATP phosphoribosyltransferase (PRPP synthetase; EC 2.4.2.17), an abnormal **amidophosphoribosyltransferase**, or deficiency of hypoxanthine phosphoribosyltransferase (EC 2.4.2.8). **Allopurinol** is useful in treatment.

gp *abbr. for* glycoprotein used in conjunction with the relative molecular mass (e.g. gp115).

gp32 an envelope glycoprotein from HIV-related viruses including **SIV** types. *See* **HIV protein**.

G1P *or* **G-1-P** *abbr. for* glucose 1-phosphate.

G6P *or* **G-6-P** *abbr. for* glucose 6-phosphate.

GPD *(in clinical chemistry) abbr. for* glucose-6-phosphate dehydrogenase.

G_0 phase G-'zero' phase; a state of withdrawal from the eukaryotic **cell-division cycle**. It occurs if no stimulus for cell division occurs during G_1 phase, leaving the cell in a quiescent G_1 phase. It is often seen in differentiated cells.

G_1 phase Gap 1 phase; the phase of the eukaryotic **cell-division cycle** between the end of **cytokinesis** and the start of DNA synthesis, i.e. the gap between M phase and S phase.

G_2 phase Gap 2 phase; the phase of the eukaryotic **cell-division cycle**, between the end of DNA synthesis and the beginning of mitosis, i.e. the gap between S phase and M phase.

GPI *(in clinical chemistry) abbr. for* glucose-6-phosphate isomerase.

GPI anchor *abbr. for* glycosylphosphatidylinositol anchor; a molecular mechanism for attaching a membrane protein to the lipid bilayer of a cell membrane. Structurally it consists of a molecule of phosphatidylinositol (*abbr.*: PI) to which is linked, via the C-6 hydroxyl of the inositol, a carbohydrate chain. This chain is in turn linked to the protein through an ethanolamine phosphate moiety, the amino group of which is in amide linkage with the C-terminal carboxyl of the protein chain, the phosphate group being esterified to the C-6 hydroxyl of the terminal mannose of the core carbohydrate chain. The carbohydrate chain varies in composition between species, but invariably contains a core tetrasaccharide, the first component of which is a glucosamine residue in glycosidic linkage with the inositol C-6 hydroxyl. The tetrasaccharide has the structure Man(α1-2)Man(α1-6)Man(α1-4)GlcNH_2. Variation frequently occurs in the presence of additional α-mannose residues on the anchors of *Trypanosoma cruzi*, yeast, slime mould, and mammalian proteins. Anchors of *Trypanosoma brucei* have more elaborate carbohydrate side-chains containing galactose, glucosamine, and sialic-acid residues. In the case of metazoan eukaryotes, additional ethanolamine phosphate substituents may occur on mannose residues, and the inositol is often palmitoylated. Biosynthesis begins with attachment of the glucosamine moiety to phosphatidylinositol, followed by sequential addition of other sugars; the GPI moiety is attached to protein during processing in the endoplasmic reticulum, the signal being a hydrophobic sequence at the C terminus, which is removed during the attachment process. GPI-anchored proteins are released from membranes by PI-specific phospholipases.

While the general function of the GPI anchor is to anchor the protein to the membrane, wider functions may include: location of the protein at specific sites, particularly the apical membrane of polarized epithelial cells; promotion of sequestration into membrane microdomains, these proteins being excluded from clathrin-associated regions but found in **caveolae**; anchoring of proteins of the glycocalyx, and cell signalling and cell recognition proteins.

In addition to protein-linked GPIs, *Leishmania* spp. also synthesize two classes of free GPIs, the polydisperse **lipophosphoglycans** (LPGs) and the low molecular mass **glycoinositolphospholipids** (GIPLs). LPGs are restricted in occurrence (e.g. promastigote stage) but GIPLs are relatively abundant on the cell surface of promastigote and amastigote stages. GIPLs are also found on the surface of many other trypanosomatid parasites, e.g. *T. cruzi*, *Leptomonas*, *Herpetomonas*, and *Phytomonas*.

gp 43 processing protease *see* **oviductin**.

G-protein guanine nucleotide binding protein; any of a family of heterotrimeric GTP-binding and hydrolysing proteins; they belong to a superfamily of GTPases that includes monomeric proteins such as EF-Tu (*see* **EF-T**) and $p21^{ras}$ (*see* **RAS**). The heterotrimeric G-proteins are a component of receptor mediated activation or inhibition of **adenylate cyclase** and other **second messenger** systems, e.g. **phosphatidylinositol cycle**. They mediate the intracellular actions of many hormones, growth factors, and cytokines. The system is widely distributed but unique to eukaryotes. G-proteins consist of three subunits; the α subunit (39–46 kDa) contains the guanine nucleotide binding site and possesses GTPase activity; the β (37 kDa) and γ (8 kDa) subunits are tightly associated and function as a $\beta\gamma$ heterodimer. α, β, and γ polypeptides are encoded by at least 16, 4, and 7 genes respectively. The classes of G-protein and subunits are subscripted: thus the α subunit of G-protein S (a stimulatory G-protein that results in activation of **adenylate cyclase**) is $G_{S\alpha}$; other G-proteins include G_i, an inhibitory **G-protein** which differs from G_S structurally (different type of α subunit) and results in inhibition of **adenylate cyclase**; the binding of **somatostatin** to its receptor results in G_i activation; G_o, a G-protein detected by cDNA probes, of wide tissue distribution in mammals but of unclear role; G_p, a G-protein that leads to activation of phospholipase C (*see* **phospholipase**), release of Ca^{2+} and activation via **calmodulin** and **protein kinase C** (*see also* **phosphatidylinositol cycle**). Binding of $G_{\alpha\beta\gamma}$ to activated receptor occurs when GDP is bound to the G-protein ($\alpha\beta\gamma$-GDP). Association of the heterotrimer with activated receptor causes exchange of GDP for GTP. Binding of GTP causes the heterotrimer to dissociate into α-GTP and $\beta\gamma$ units, either of which may interact with an effector. The GTPase activity of α yields α-GDP which inactivates it. α-GDP has a high affinity for $\beta\gamma$ thus reforming $\alpha\beta\gamma$-GDP which is once again available for association with an activated receptor. G_T, *see* **transducin**. Examples: $G_{S\alpha}$ from human and dog: database code GBAS_HUMAN, 394 amino acids (45.61 kDa); β subunit from G_S and transducin (human): database code GBB2_HUMAN, 340 amino acids (37.29 kDa): γ brain and adrenal form for G_S, G_i, G_o (bovine): database code GBG2_BOVIN, 71 amino acids (7.84 kDa). *See also* **Appendix E**.

GPT *(in clinical chemistry) abbr. for* glutamate–pyruvate transaminase (EC 2.6.1.2) (ALT preferred).

G-quartet *or* **G-tetrad** a cyclic H-bonded array of guanines that can occur in both RNA and DNA to form a quadruple helix structure. Sequences that form such structures are found in telomeric sites, the switch regions of immunoglobulin heavy-chain genes, and elsewhere. *See* **KEM1**.

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Gra *symbol for* a residue of **glyceraldehyde**.

Graafian follicle a spherical vesicle occurring in the mature mammalian ovary and in which the ovum develops. When the ovum matures it is discharged after rupture of the follicle, which is then transformed into a **corpus luteum**. [After Reijnier (Regnier) de Graaf (1641–73), Dutch physician and anatomist.]

grade **1** a degree or position in a scale, as of quality, size, etc., e.g. analytical grade, commercial grade. **2** a unit of angle equal to one-hundredth of a right angle, i.e. 0.9°.

gradient the change in the value of a specified (chemical or physical) property or value per unit distance in a specified direction.

gradient elution a chromatographic elution procedure in which the concentration of a component of the eluent is increased continuously. The gradient may be linear, concave – i.e. increasing slowly at first and more rapidly as elution proceeds – or convex – i.e. increasing rapidly at first and more slowly as elution proceeds. More complex or discontinuous (stepped) elution gradients are sometimes used.

gradient former *or* **gradient mixer** any device for producing solutions of varying, but defined, composition containing one or more components.

gradient gel electrophoresis *or* **gradient acrylamide gel electrophoresis** *or* **polyacrylamide gradient gel electrophoresis** (*abbr.*: PAGE) a type of **zone electrophoresis** in which the supporting medium is a pore-gradient gel, i.e. one where an increasing concentration of polyacrylamide in the direction of electrophoretic mobility decreases the sizes of the pores in the gel in that direction to the point where molecules of more than a certain size are prevented from moving further in the electric field. The concentration gradient may be either discontinuous, i.e. stepped, or continuous. Advantages of the technique over electrophoresis in uniform gels (*see* **gel electrophoresis**) are sharper zones and an ability to resolve, on a single gel, mixtures of macromolecules of a wider range of sizes.

gradient layer *or* **gradient packing** a chromatographic layer, or column packing, incorporating a continuous change of some property that affects separations, e.g. a pH gradient or a pore gradient.

graft **1** any part of an organism, animal or plant, that is inserted into and unites with a larger part of another or the same organism. **2** to transplant (tissue) to another organism or to another site on the same organism.

graft versus host disease a condition where immunocompetent donor cells recognize and react against the recipient's tissues, because the recipient is immunosuppressed or cannot recognize the different genetic constitution of the donor cells.

Graham, Thomas (1805–69), Scottish chemist, one of the founders of physical chemistry; he conducted research on absorption of gases, osmosis, diffusion, colloids, and dialysis.

Graham's law of diffusion a law stating that at equal temperatures and pressures the rates of diffusion of gases are inversely proportional to the square roots of their densities and hence to the square roots of their relative molecular masses (M_rs). Thus for two gases A and B,

$$J_A/J_B = \bar{v}_A/\bar{v}_B = M_{rB}^{1/2}/M_{rA}^{1/2},$$

where J_A and J_B, $\bar{v}_A$ and $\bar{v}_B$, and M_{rA} and M_{rB} are the fluxes, mean velocities, and relative molecular masses of A and B, respectively.

grain **1** any small, hard particle, e.g. a grain of sand. **2** any simple single-seeded indehiscent fruit in which the seed wall fuses with the carpel wall during development. Technically called a **caryopsis**, it is typical of the cereals and other grasses. **3** *(in photography)* any of the many particles of silver halide in a photographic emulsion. The resolution possible in the image is inversely proportional to the grain size in the emulsion. **4** any of the dried insect bodies present in dyes such as cochineal.

gram *symbol*: g; a unit of mass equal to a thousandth part of the **kilogram** in both the Système International (SI) and the metric system (cgs or mks) of units.

+gram *comb. form* indicating a drawing, something written or recorded; the record produced by an instrument, e.g. spectrogram; the visible result of a procedure, e.g. autoradiogram, chromatogram.

gram-atom *or* **gram-atomic weight** *abbr.*: g-atom; the atomic weight of an element expressed in grams; it has now been replaced by amount of substance, measured in **moles**.

gram-equivalent *or (formerly)* **gram-equivalent weight** *abbr.*: g-equiv; an **equivalent** (def. 3) expressed in grams.

gramicidin any of a group of linear polypeptide antibiotics that are active against Gram-positive microorganisms and are isolated from cultures of *Bacillus brevis*. The commercial material is a mixture of gramicidins A, B, C, and D, all of which consist of chains of 15 amino-acid residues in a pattern of alternating D- and L-forms; all have a formyl group at the N terminus and an ethanolamine residue at the C terminus. Gramicidins increase the permeability of biological membranes to protons and alkali-metal cations by forming transient dimeric ionophoric channels through the membrane. *See also* **gramicidin S**.

gramicidin S a homodetic cyclic decapeptide antibiotic, *cyclo*(-Val-Orn-Leu-DPhe-Pro-Val-Orn-Leu-DPhe-Pro-), produced by a strain of *Bacillus brevis* and active against Gram-positive bacteria. Gramicidin S is more closely related to **tyrocidins** in its biological and chemical properties than to true **gramicidins**. Its biosynthesis occurs by a mechanism that is not dependent on the presence of ribosomes or mRNA. It was the first peptide antibiotic to be chemically synthesized, and is so named because it was first isolated in Soviet Russia, where it was widely used.

gram-molecule *or* **gram-molecular weight** *symbol*: g-mol; the molecular weight of a compound (or element) expressed in grams; it has now been replaced by the **mole**.

Gram-negative describing a bacterial cell that, during **Gram staining**, does not retain the basic dye in its cell wall. The walls of Gram-negative organisms are thin, about 10 nm across, but complex, having a lipopolysaccharide layer outside the peptidoglycan layer; they are also resistant to digestion by lysozyme. *Compare* **Gram-positive**.

Gram-positive describing a bacterial cell that, during **Gram staining**, retains the basic dye in its cell wall. The walls of Gram-positive organisms are relatively thick, 15–80 nm across, and consist of a network of peptidoglycan; they are readily digested by lysozyme. *Compare* **Gram-negative**.

Gram staining *or* **Gram stain** a staining procedure used for bacteria in which the cells are first heat-fixed and stained with a basic dye, e.g. Crystal Violet, then treated with I_2–KI solution to fix the stain, washed with ethanol or acetone, and finally counterstained with another dye, e.g. carbolfuchsin or safranin. Cells that retain the basic dye after this procedure are called **Gram-positive**; those that do not are called **Gram-negative**. [After Hans Christian Joachim Gram (1853–1938), Danish physician and bacteriologist, who described the method in 1884.]

grancalcin a Ca^{2+}-binding protein containing four **EF hands** and abundant in neutrophils and monocytes. It exhibits strong homology to **sorcin**. It is a homodimer. Example from human: database code A42578, 217 amino acids (23.98 kDa).

β granin *see* **chromogranin**.

Granit, Ragnar Arthur (1900–91), Finnish-born Swedish neurophysiologist; Nobel Laureate in Physiology or Medicine (1967) jointly with H. K. Hartline and G. Wald 'for their discoveries concerning the primary physiological and chemical visual processes in the eye'.

granular *or* **granulose** *or* **granulate** being composed of, or having the character of small particles or **grains** (def. 1).

granular endoplasmic reticulum *or* **rough endoplasmic reticulum** *see* **endoplasmic reticulum**.

granulate **1** to make (something) into **grains** (def. 1). **2** (of a wound, ulcer, etc.) to form **granulation tissue**. **3** *another word for* **granular**.

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granulation 1 the act or process of subdividing a solid into small, usually rounded **grains** (def. 1). 2 the formation of one or more small, rounded lumps (grains (def. 1)) in a tissue. 3 the development of **granulation tissue**.

granulation tissue the mass of young connective tissue and blood vessels formed on the surface of a wound or ulcer in the early stages of healing.

granule any small **grain** (def. 1), especially any small intracellular particle containing stored material that can be seen by (electron) microscopy, e.g. insulin-containing β granules in the B cells of the islets of Langerhans, starch granules in potato tubers.

granulocyte a category of white blood cells distinguished by the presence of conspicuous cytoplasmic granules. Granulocytes include **neutrophils**, **basophils**, and **eosinophils**.

granulocyte-colony stimulating factor *see* **colony stimulating factor**.

granulose 1 *another word for* **granular**. 2 *an obsolete name for* **starch** or amylose.

granum (*pl.* **grana**) a stack of disclike **thylakoids** resembling a pile of coins. Grana occur in **chloroplasts**, especially in higher plants.

granzyme A enzyme of sub-subclass EC 3.4.21; *other names*: cytotoxic T-lymphocyte proteinase 1; Hanukkah factor (HF); granzyme 1; CTL tryptase; fragmentin 1; trypsin-like serine proteinase. An enzyme necessary for target-cell lysis in cell-mediated immune responses; it cleaves on the carbonyl side of Lys or Arg. It may be involved in **apoptosis**. It occurs in cytoplasmic granules. The molecule is a homodimer, disulfide linked. Example (precursor) from human: database code GRAA_HUMAN, 262 amino acids (28.93 kDa).

grape sugar *a former name for* D-glucose. *See* **glucose**.

graph 1 a diagram showing the relation between two variable quantities, or the relation between a mathematical function and different values of one of the variables in the function, usually plotted between axes at right angles to each other. 2 to plot or draw a graph.

+graph *comb. form* 1 denoting (something) drawn, recorded, or written (in the way specified), e.g. autoradiograph, photograph. 2 denoting an instrument or device that draws or records (observations), e.g. spectrograph. 3 denoting the act or process of producing such a drawing or record. *Compare* **+gram**. —**+graphic** *or* **+graphical** *adj. comb. form.*

graphics *(functioning as sing.)* 1 the use of diagrams in calculation. 2 the production of diagrams, representations of molecular structures, etc., often by computer.

+graphy *comb. form* denoting a method, process, or technique that produces a drawing or record, e.g. chromatography. *See* **+graph**.

grating *see* **diffraction grating**.

Graves' disease *or* **Basedow's disease** a disease characterized by diffuse goitre, thyrotoxicosis, and exophthalmia. It is an autoimmune condition associated with the presence of thyroid-stimulating antibodies in the blood. [After Robert James Graves (1796–1853), Irish physician.]

Graves' disease carrier protein see **GDC**.

gravimetric analysis quantitative analysis of the chemical composition of substances or materials based on the separation of each component of interest and weighing either the purified compound or a derivative of it.

gravimetry measurement by weighing. —**gravimetric** *or* **gravimetrical** *adj.*

gravitation the attractive force that bodies exert on one another as a result of their mass; any process or result caused by such an attractive force. —**gravitational** *adj.*

gravitational constant *symbol*: *G*; the proportionality constant relating the attractive force, *F*, between two bodies of mass m_1 and m_2, and the distance between them, *s*, in Newton's law of gravitation:

$$G = Fs/m_1m_2 = 6.672\ 59\ (85) \times 10^{-11}\ m^3\ kg^{-1}\ s^{-2}.$$

gravitational field any **field** (def. 1) associated with a mass by which a force is exerted on a second mass placed in this field.

gravitational interaction any interaction between bodies or particles that results from their masses.

gravitational mass *see* **mass**.

gravity 1 the attractive force that moves or tends to move bodies towards the centre of any celestial body such as the Earth or the Moon. 2 the attribute of having weight. 3 **specific gravity**.

gray *symbol*: Gy; the SI derived unit of **absorbed dose** of radiation, equal to one joule per kilogram of living tissue;

$$1\ Gy = 1\ J\ kg^{-1} = 1\ m^2\ s^{-2}.$$

Compare **sievert**. *See also* **rad**. [After Louis Harold Gray (1905–65), British physicist and radiobiologist.]

Grb2 growth factor receptor-bound protein 2; *also called* **Ash protein**; a cytoplasmic protein, related to sem-5 (*see* ***sem-5***), that participates in downstream signalling after activation of a variety of cell receptors. It binds directly to activated epidermal growth factor and platelet-derived growth factor receptors; indirectly it can be recruited by G-protein-coupled receptors through tyrosine phosphorylation of Shc (*see* **SHC**). Grb2 binds to activated Shc and the complex then recruits Sos (*see* ***sos***). The Shc–Grb2–Sos complex binds to the plasma membrane where Sos catalyses **Ras** guanine nucleotide exchange, leading to MAP kinase activation. Example from human (identical in rat): database code GRB2_HUMAN, 217 amino acids (25.18 kDa).

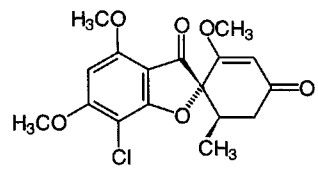
GRE *abbr. for* glucocorticoid response element.

GRF *abbr. (sometimes) for* growth hormone releasing factor (i.e. **GHRH**).

Gri *symbol for* glyceric acid *or* glycerate.

grid 1 a framework made up of fine wires arranged in two sets at right angles to each other, especially a device for supporting the specimen in an electron microscope. 2 an electrode controlling the current flowing through a thermionic valve.

griseofulvin [2*S*]-*trans*-7-chloro-2′,4,6-trimethoxy-6′-methylspiro[benzofuran-2(3*H*),1′-(2)cyclohexene]-3,4′-dione; a chlorine-containing **polyketide** metabolite of *Penicillium griseofulvum* and *P. janczewskii*. It has antifungal properties and is used therapeutically, e.g. for treatment of ringworm. It inhibits spindle formation in mitosis, microtubule function, and possibly nucleic-acid synthesis.



Grn *symbol for* glycerone.

gRNA *abbr. for* guide RNA; small RNA molecules, 60–80 nucleotides long, that may be involved in editing of RNA by supplying information concerning nucleotide deletion or addition. *See also* **editosome**.

gro the symbol for any of a group of related genes found in bacteria (especially *Escherichia coli*), mutations in which affect the growth of phages.

Gro *symbol for* glycerol.

groEL the symbol for any of a family of bacterial genes encoding **chaperonins**. They have eukaryotic counterparts. Example of a *groEL* protein product from *Escherichia coli*: oligomer of 14 subunits composed of two stacked rings of seven subunits; it has ATPase activity; database code CH60_ECOLI, 547 (57.02 kDa).

groES the symbol for any of a family of bacterial genes encoding **chaperonins**. They have eukaryotic counterparts. Example of a *groES* protein product from *Escherichia coli*: six to eight subunits arranged in a ring; it binds to the ***groEL*** protein prod-

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uct to suppress the latter's ATPase activity; database code CH10_ECOLI, 97 amino acids (10.38 kDa)

Grotthus and Draper law a law stating that only those radiations absorbed by a system are effective in producing chemical change in the system.

groundplasm *or* **cytoplasmic matrix** the sub-electron-microscopic material of the **cytoplasm**, excluding the cell organelles, cell particles, and other microscopically resolvable structures. It contains the cytoplasmic enzymes and metabolites together with components of the **cytoskeleton**.

ground state the state of lowest energy of any system.

ground substance *an alternative name for* the **matrix** (def. 2) of connective tissue.

ground tissue *a collective term for* plant tissue other than the epidermis or peridermis and vascular tissue.

group *(in chemistry) or (formerly)* **radical 1** any defined continuously linked collection of atoms within a molecular entity. In organic chemical nomenclature the meaning within this general sense is restricted to any covalently bonded collection of atoms that behaves as a unit in chemical reactions; **functional group**, **substituent group**. **2** any of the columns of chemical elements in the **periodic table**. **3** a **blood group**.

group p*K* the p*K* of a specific group in a molecule with two or more acid groups. In general the term applies only to a particular ionic form of the molecule, because the p*K* of a group changes when any other group in the molecule changes its ionization state, and thus changes as the substance is titrated. *Compare* **molecular p*K***, **titration p*K***.

group potential the tendency of a **group** (def. 1) to escape from a molecular entity.

group-transfer potential the Gibbs energy change (free energy change, ΔG) occurring when a **group** (def. 1) is transferred from a donor compound to the nucleophile water, i.e. when the group is removed by hydrolysis of the donor. It reflects the thermodynamic tendency for the group to be transferred.

group-transfer reaction any chemical reaction in which a **group** (def. 1) is transferred from a donor compound to an acceptor compound. Such reactions may be catalysed by a **transferase** enzyme of EC class 2.

group translocation any process in which a substance to be transported across a biological membrane undergoes covalent modification prior to crossing the membrane.

growth curve the change, as a function of time, in the number of cells of a growing culture or in some measure of the size of an organism.

growth factor **1** any specific substance that must be present in a culture medium for multiplication of the cultured cells to take place. **2** a specific substance that is a necessary constituent of the diet for the normal growth of a particular animal, or is required in the soil for the normal growth of a particular plant.

growth factor receptor-bound protein 2 *see* **Grb2**.

growth hormone *another name for* **somatotropin**.

growth hormone inhibitory factor *abbr.*: GHIF *or* GIF; *a former name for* **somatostatin**.

growth hormone release-inhibiting hormone *abbr.*: GH-RIH; *a former name for* **somatostatin**.

growth hormone releasing factor *abbr.*: GHRF *or* GRF; *another name for* **GHRH**.

growth hormone releasing hormone *see* **GHRH**.

GRP *see* **Grb2**.

GRP 75 *see* **mortalin**.

GRS *(in clinical chemistry) abbr. for* β-glucuronidase.

Grunstein–Hogness procedure *an alternative name for* **colony hybridization**.

GSH *abbr. for* glutathione.

GSSG *abbr. for* oxidized glutathione (*see* **glutathione**).

GST *abbr. for* glutathione S-transferase (*see* **glutathione transferase**).

GST fusion protein a **fusion protein** in which a synthetic oligonucleotide of a defined sequence of the protein of interest is grafted onto the glutathione transferase (GST) gene. The fused protein is then expressed in a recombinant system, purified by **affinity chromatography** (making use of the properties of GST), and the GST removed to release the pure protein.

GT–AG rule a rule stating that in RNA there is a requirement for a GT at the 5′ side of a splice junction and an AG at the 3′ side.

GTD *(in clinical chemistry) abbr. for* glutathione reductase.

G-tetrad *an alternative name for* **G-quartet**.

GTF *abbr. for* glucose-tolerance factor.

GTP *abbr. for* guanosine triphosphate.

GTPase any enzymic activity that hydrolyses GTP to GDP and orthophosphate. It is associated with **G-proteins**, **EF-Ts**, and **HIV protein**.

GTP-binding protein any of various proteins that bind GTP as a regulatory molecule. This binding is frequently associated with a **GTPase** activity. GTP-binding proteins include elongation and initiation factors (e.g. **EF-Tu**), **G-proteins**, G25K GTP-binding protein, **Ras proteins**, and yeast CDC42 (*see* **CDC markers**). Binding of GTP normally activates the protein, an effect that is reversed by hydrolysis of the GTP to GDP. Example from human: database code G25B_HUMAN, 191 amino acids (21.29 kDa).

GTP[S] *or* **GTPγS** *abbr. for* guanosine 5′-γ-thiotriphosphate.

GTR1 a representative 12-transmembrane domain transport protein that effects the facilitated diffusion of glucose in certain mammalian tissues. Example from human erythrocytes: database code GTR1_HUMAN, 492 amino acids (54.04 kDa).

GTT *abbr. for* glucose tolerance test.

Gu *symbol for* guanidine.

Gua *symbol for* a residue of the purine base guanine (alternative to G).

GUA a codon in mRNA for L-valine.

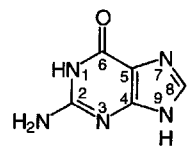
guanidine *symbol*: Gu; the strongly basic substance, iminourea; aminomethanamidine; $(H_2N)_2C{=}NH$.

guanidinium the cation, $[C(NH_2)_3]^+$, derived from guanidine by uptake of a hydron.

guanidino the amidinoimino group, $-HN-C(=NH)-NH_2$, derived from guanidine.

guanidinoacetate *N*-methyltransferase EC 2.1.1.2; an enzyme of the pathway for *de novo* synthesis of **creatine**, by reaction of *S*-adenosyl-L-methionine with guanidinoacetate releasing *S*-adenosyl-L-homocysteine. Example from rat: database code GAMT_RAT, 235 amino acids (26.25 kDa).

guanine *symbol*: G *or* Gua; 2-amino-6-hydroxypurine; 2-amino-1,7-dihydro-6*H*-purin-6-one; a purine that is one of the five main bases found in nucleic acids and a component of a number of phosphorylated guanosine derivatives whose metabolic or regulatory functions are important.



guanine nucleotide binding protein *see* **GTP-binding protein**.

guanine nucleotide releasing protein *abbr.*: GNRP; *or* **guanine nucleotide releasing factor**, *abbr.*: GRF; a protein that binds to a Ras protein (*see* **Ras family of proteins**) or Ras-related **GTP-binding protein** and activates it by stimulating it to release its bound GDP and bind GTP in its place. The C-terminal 310 amino acids show homologies to Cdc25 (*see* **cdc gene**) and Sos, the product of ***sos***. Example from *Rattus norvegicus*: database code GNRP_RAT, 1244 amino acids (142.67 kDa).

guanosine *symbol*: G *or* Guo; guanine riboside; 9-β-D-ribofuranosylguanine; a **nucleoside** with a wide species distribution.

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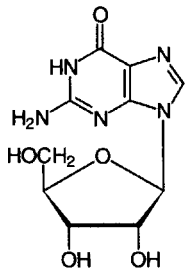
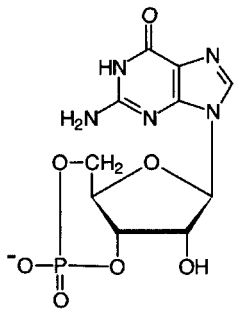


guanosine

guanosine 2′,3′-(cyclic)phosphate *see* **guanosine phosphate**.

guanosine 3′,5′-(cyclic)phosphate *or* guanosine 3′,5′-cyclophosphate *see* **guanosine 3′,5′-phosphate**.



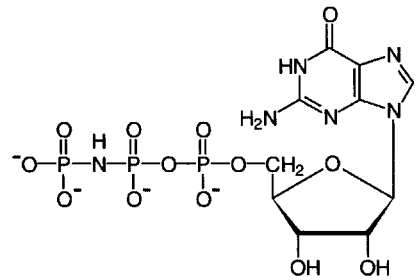
guanosine 5′-diphosphate *symbol*: Guo5′*PP or* ppG; *the recommended name for* guanosine diphosphate (*abbr.*: GDP), 5′-diphosphoguanosine, 5′-guanylyl phosphate, guanosine 5′-(trihydrogen diphosphate), a universally distributed nucleotide that occurs in both the free state and as a component of **guanosinediphosphosugars**. It is a metabolic precursor of guanosine 5′-triphosphate, GTP, and is a substrate, a product, or a regulatory agent in many metabolic systems.

guanosine 3′-diphosphate 5′-diphosphate *symbol.*: ppGpp; *see* ***relA***, ***spoT***.

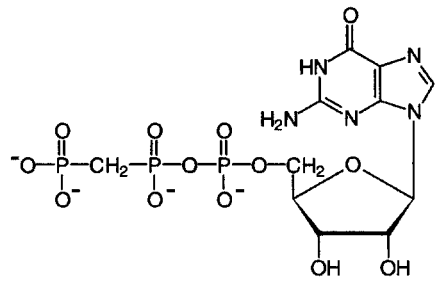
guanosinediphosphomannose *or* **guanosine(5′)diphospho(1)-α-D-mannose** *symbol*: Guo*PP*Man; *the alternative recommended names for* guanosine diphosphate mannose (*abbr.*: GDPM *or* GDPmannose); guanosine 5′-(α-D-mannopyranosyl diphosphate); α-D-mannopyranosyl 5′-guanylyl phosphate; the most important **guanosinediphosphosugar**. It is synthesized from α-D-mannose 1-phosphate and guanosine 5′-triphosphate by the action of **mannose-1-phosphate guanylyltransferase** (EC 2.7.7.13). It is an intermediate in the synthesis of mannose-containing homo- and heteroglycans in plants. In animal cells GDPmannose is an intermediate in the incorporation of residues of both mannose and fucose into *N*-linked oligosaccharides of glycoproteins, its conversion to GDP-L-fucose having first taken place in the case of fucose.

guanosinediphosphosugar *or* **guanosine diphosphate sugar** *abbr.* GDPsugar; any of several **nucleosidediphosphosugars** in which the distal phosphoric residue of guanosine 5′-diphosphate is in glycosidic linkage with a monosaccharide (or a derivative of a monosaccharide). Included are GDP-L-fucose, GDP-D-glucose, GDP-L-guluronic acid, GDP-D-mannose (*see* **guanosinediphosphomannose**), and GDP-D-mannuronic acid.

guanosine 5′-[β,γ-imido]triphosphate *symbol*: Guo*PP*[NH]*P or* p[NH]ppG; *the recommended name for* β,γ-imidoguanosine 5′-triphosphate (*abbr.*: GTP[β,γ-NH]), 5′-guanylyl imidodiphosphate (*abbr.*: GMP-PNP), 5′-guanylyl iminodiphosphonate, guanosine (5′→O^3)-1,2-μ-imidotriphosphate, a synthetic nonhydrolysable analogue of guanosine triphosphate, GTP, in which the oxy group between the latter's intermediate and terminal phosphorus atoms is replaced by an imido group. It stimulates G-proteins and systems activated thereby.



guanosine 5′-[β,γ-methylene]triphosphate *symbol*: Guo*PP*[CH_2]*P or* p[CH_2]ppG; *the recommended name for* β,γ-methyleneguanosine 5′-triphosphate, (*abbr.*: GTP[β,γ-CH_2]), 5′-guanylyl methylenediphosphonate (*abbr.*: GMP-PCP), guanosine (5′→O^3)-1,2-μ-methylenetriphosphate, a synthetic nonhydrolysable analogue of guanosine 5′-triphosphate, GTP, in which the oxy group between the latter's intermediate and terminal phosphorus atoms is replaced by a methylene group. It is an effective activator of ADP-ribosylation factor but not of G_S (*see* **G-protein**).



guanosine monophosphate *abbr.*: GMP; *an alternative name for* any guanosine phosphate, but in particular for **guanosine 5′-phosphate**, especially when its distinction from guanosine (5′-)-diphosphate and guanosine (5′-)triphosphate requires emphasis.

guanosine phosphate *symbol*: Guo*P*; guanosine monophosphate (*abbr.*: GMP); any phosphoric monoester or diester of guanosine. There are three monoesters – guanosine 2′-phosphate, guanosine 3′-phosphate, and **guanosine 5′-phosphate** – and two diesters – guanosine 2′,3′-phosphate and **guanosine 3′,5′-phosphate** – although guanosine 5′-phosphate, guanylic acid is the ester commonly denoted (the locant being omitted if no ambiguity may arise). Guanosine 2′,3′-phosphate (*symbol*: Guo-2′,3′-*P*), also named guanosine 2′,3′-(cyclic)phosphate *or* cyclic guanosine 2′,3′-monophosphate (*abbr.*: 2′,3′-cyclic GMP), is formed as an intermediate during the alkaline hydrolysis of ribonucleic acid. This diester then readily hydrolyses to a mixture of the two monoesters guanosine 2′-phosphate (*symbol*: Guo2′*P*), also named guanosine 2′-monophosphate (*abbr.*: 2′GMP) *or* 2′-guanylic acid *or* guanylic acid a, and guanosine 3′-phosphate (*symbol*: Guo3′*P*), also named guanosine 3′-monophosphate (*abbr.*: 3′GMP) *or* 3′-guanylic acid *or* guanylic acid b.

guanosine 2′-phosphate *see* **guanosine phosphate**.

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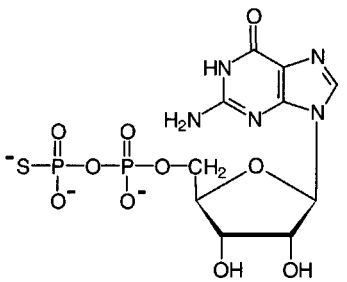
guanosine 2′,3′-phosphate *see* **guanosine phosphate**.

guanosine 3′-phosphate *see* **guanosine phosphate**.

guanosine 3′,5′-phosphate *symbol*: Guo-3′,5′-*P*; *the recommended name for* cyclic guanosine 3′,5′-monophosphate (*abbr.*: 3′,5′-cyclic GMP *or* cyclic GMP *or* cGMP), guanosine 3′,5′-cyclophosphate, guanosine 3′,5′-(cyclic) phosphate, a monophosphoric diester of guanosine found in practically all mammalian tissues. It is a cyclic nucleotide similar in structure and the regulation of its metabolism to **adenosine 3′,5′-phosphate**, cyclic AMP, but the levels in tissues are commonly less than 5 percent of those of cyclic AMP. Also like cyclic AMP, it acts as a **second messenger** in many systems, and it activates a number of distinct cyclic-GMP-dependent protein kinases that share some of their properties with their cyclic AMP counterparts; in some instances it antagonizes the action of cyclic AMP. Cyclic GMP is produced by the action of **guanylate cyclase** on guanosine 5′-triphosphate, GTP, and it mediates signal transduction for systems that activate this enzyme.

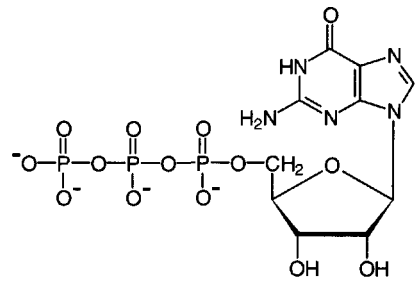
guanosine 5′-phosphate *or* **5′-guanylic acid** *or* **5′-phosphoguanosine** *or* **5′-*O*-phosphonoguanosine** *symbol*: Guo5′*P*; *alternative recommended names for* guanosine 5′-monophosphate (*abbr.*: 5′GMP), guanosine 5′-(dihydrogen phosphate), guanine (mono)ribonucleotide. (The locant is commonly omitted if there is no ambiguity as to the position of phosphorylation.) It is biosynthesized from inosine 5′-phosphate, 5′-inosinic acid, via xanthosine 5′-phosphate and also from free guanine by the **salvage pathway**.

guanosine 5′-β-thiodiphosphate *symbol*: Guo5′*PP*[S] *or* [S]ppG; *the recommended name for* guanosine 5′-[β-thio]diphosphate (*abbr.*: GDPβS), guanosine 5′-(2-thiodiphosphate) (*abbr.*: GDP[S]), guanosine (5′→O^2)-1-thiodiphosphate, a synthetic nonhydrolysable analogue of guanosine 5′-diphosphate, GDP, in which an oxygen atom of its terminal phosphoric residue is replaced by a sulfur atom. It is a competitive inhibitor of the activation of G-proteins by guanosine 5′-triphosphate and of the stimulation of adenylate cyclase by guanosine 5′-triphosphate and fluoride.



guanosine 5′-γ-thiotriphosphate *symbol*: Guo*PPP*[S] *or* [S]pppG; *the recommended name for* guanosine 5′-[γ-thio]triphosphate (*abbr.*: GTP-γ-S), guanosine 5′-(3-thiophosphate) (*abbr.*: GTP[S]), guanosine (5′→O^3)-1-thiotriphosphate, a synthetic nonhydrolysable analogue of guanosine 5′-triphosphate, GTP, in which an oxygen atom of its terminal phosphoric residue is replaced by a sulfur atom. It is used in membrane studies to stimulate G-proteins and in studies of DNA synthesis.

guanosine 5′-triphosphate *symbol*: Guo5′*PPP or* pppG; *the recommended name for* guanosine triphosphate (*abbr.*: GTP), 5′-triphosphoguanosine, 5′-guanylyl diphosphate, guanosine 5′-(tetrahydrogen triphosphate), an important coenzyme and enzyme regulator present in all cells. It is formed from guanosine 5′-diphosphate by substrate-level phosphorylation or by transfer of the terminal phosphoric residue from **adenosine 5′-triphosphate** through the action of nucleoside-diphosphate kinase (EC 2.7.4.6). Reactions in which GTP participates are often driven in the direction leading to hydrolysis, the free energy change then being utilized for energy-requiring purposes, e.g. microtubule assembly or protein biosynthesis. GTP also participates in various synthetic reactions by the transfer of a phosphoric residue to other metabolites, e.g. to oxaloacetate to form phospho*enol*pyruvate in gluconeogenesis.



guanosyl any chemical group formed by the loss of a 2′-, a 3′-, or a 5′-hydroxyl group from the ribose moiety of guanosine. *Compare* **guanylyl**.

guanyl *misnomer for* **1 guanylyl**. **2 guanylate**.

guanylate **1** the mono- or the di-anion of **guanylic acid**. **2** any mixture of guanylic acid and its anions. **3** any salt or ester of guanylic acid.

guanylate cyclase EC 4.6.1.2; *systematic name*: GTP pyrophosphate-lyase (cyclizing); *other names*: guanylyl cyclase (not recommended but often used); guanyl cyclase (incorrect). A phosphorus–oxygen lyase enzyme that catalyses the elimination of pyrophosphate from guanosine 5′-triphosphate, GTP, by formation of guanosine 3′,5′-phosphate, cyclic GMP. There are two types: (1) a soluble form, which exists as a heterodimer of α and β chains; human examples: α-3, database code CYG5_HUMAN, 717 amino acids (81.28 kDa); β-1, database code CYG1_HUMAN, 619 amino acids (70.43 kDa); and (2) a membrane-bound form, typical of some receptors; e.g. human atrial **natriuretic peptide receptor** A (precursor): database code ANPA_HUMAN, 1061 amino acids (118.78 kDa).

guanyl cyclase *incorrect name for* **guanylate cyclase**.

guanylic acid *the trivial name for* any phosphoric monoester of guanosine. The position of the phosphoric residue on the ribose moiety of a given ester may be specified by a prefixed locant. *See* **guanosine phosphate**. However, 5′-guanylic acid is the ester commonly denoted, its locant usually being omitted if no ambiguity may arise. 5′-Guanylic acid is also an alternative recommended name for **guanosine 5′-phosphate**.

guanylin a pentadecapeptide hormone from rat jejunum that activates the **guanylate cyclase** component of the intestinal heat-stable **enterotoxin** receptor.

guanylyl the guanosine[mono]phospho group; the acyl group derived from **guanylic acid**.

guanylylation the process of introducing guanylyl groups into a substance.

guanylyl cyclase *see* **guanylate cyclase**.

guaran a mucilaginous **galactomannan** of ≈220 kDa that serves as a storage polysaccharide in the seeds of guar and is the prime constituent of **guar gum**. It consists of long chains of (1→4)-linked β-D-mannopyranose residues, to every alternate one of which a single α-D-galactopyranose residue is attached in (1→6)-linkage.

guard cell either of a pair of crescent-shaped cells that surround a **stoma** in plants.

guard column a small column fitted in front of the main column as a device to prolong the life of columns in high-performance liquid chromatography by removing from the sample any particulate matter, aggressive agents, or components that bind irreversibly to the column packing.

guar gum a greyish-white powder consisting predominantly of

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the polysaccharide **guaran** and obtained by grinding the endosperm of the seeds of guar, an Indian leguminous plant, *Cyamopsis tetragonoloba* (*psoralioides*), also called cluster bean. It hydrates and disperses readily in cold water to give colloidal solutions of very high viscosity that are stable over a very wide pH range and have very good suspending and lubricating properties. It is used for sizing paper and textiles, and as a stabilizing, suspending, and thickening agent in the food and pharmaceutical industries, etc. It has also been suggested as a nonabsorbable dietary additive to improve glycemic control in diabetes mellitus, possibly by slowing the uptake of ingested absorbable carbohydrate.

GUC a codon in mRNA for L-valine.

GUG a codon in mRNA for L-valine.

Guggenheim plot a procedure that makes it possible to obtain rate constants for first-order reactions when neither the initial nor the final reactant concentrations are known. Measurements of the concentration of the reactant (or of some physical quantity that measures it), c_1, c_2, c_3,...c_n, are made at times t_1, t_2, t_3,...t_n and also at times $(t_1 + \delta t)$, $(t_2 + \delta t)$, $(t_3 + \delta t)$,...$(t_n + \delta t)$, when the concentrations of the reactant are c_1', c_2', c_3',...c_n', where δt is a constant time difference, then

$$\ln(c_i - c_i') = \ln(c_0 - c_\infty)(1 - e^{-k\delta t}) - kt,$$

or

$$\ln(c_i - c_i') = \text{a constant} - kt_i,$$

hence a plot of $\ln(c_i - c_i')$ versus t_i has a slope of $-k$. [After Edward Armand Guggenheim (1901–70), British physical chemist.]

guide RNA *see* **gRNA**.

Guillemin, Roger Charles Louis (1924–), French-born US physician and endocrinologist; Nobel Laureate in Physiology or Medicine (1977) jointly with A. V. Schally 'for their discoveries concerning the peptide hormone production of the brain' [prize shared with R. S. Yalow].

guinea pig any of several species of wild or domesticated hystricomorph rodents, or cavies, in the genus *Cavia*, especially *Cavia porcellus*, which is widely used in biomedical research and testing.

Guinier plot a method of plotting the results of small-angle X-ray scattering to obtain the radius of gyration of a molecule, r_G, in the absence of information about the relative molecular mass of the component in question. It can be shown that

$$\ln(I_\theta/I_0) = -(4\pi r_G \sin\theta/\lambda)^2/3,$$

where I_θ and I_0 are the intensities of the scattered radiation at angles θ and 0 respectively, and λ is the wavelength of the radiation; hence a plot of $\ln(I_\theta/I_0)$ versus $-(4\pi\sin\theta/\lambda)^2/3$ will yield r_G.

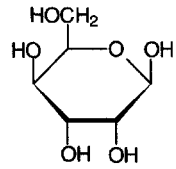
Gul *symbol for* a residue (or sometimes a molecule) of the aldohexose gulose.

GulA *symbol for* a residue (or sometimes a molecule) of the uronic acid guluronic acid.

gulo- *prefix (in chemical nomenclature)* indicating a particular configuration of a set of (usually) four contiguous >CHOH groups, as in the acyclic form of D- or L-gulose. *See* **monosaccharide**.

L-gulonolactone oxidase EC 1.1.3.8; *other name*: L-gulono-γ-lactone oxidase; a flavoprotein enzyme that catalyses the oxidation by dioxygen of L-gulono-1,4-lactone to L-*xylo*-hexulonolactone (I) and H_2O_2. I isomerizes spontaneously to L-ascorbate. The flavin is FAD. The enzyme is essential for the formation of ascorbate, and a deficiency of the enzyme, as in humans, results in dependency on a dietary supply of ascorbate (*see* **ascorbic acid**). Example from rat: GGLO_RAT, 439 amino acids (50.42 kDa).

gulose *symbol*: Gul; *the trivial name for* the aldohexose *gulo*-hexose; a stereoisomer of glucose in which the configurations at both C-3 and C-4 are inverted. There are two enantiomers. (Illustrated opposite.)



gulose (β-D-pyranose form)

guluronic acid *symbol*: GulA; the **uronic acid** resulting from the oxidation of the hydroxymethylene group at C-6 of gulose to a carboxyl group. L-Guluronic acid is a component of **alginic acid**.

gum any of numerous water-soluble or water-dispersible heteroglycans, frequently containing uronic acids, that are produced as exudates from certain plants, especially trees, following physical injury. Gums are tacky, slimy substances that harden when dry. *See also* **gum arabic**, **gum ghatti**.

gum arabic a **gum** exuded from trees of the genus *Acacia*. Structurally it is a heteroglycan containing D-galactose, L-arabinose, L-rhamnose, and D-glucuronic acid. It is used in industry, e.g. in the manufacture of thickening agents, emulsifiers, inks, and pills. It is also used in glues and pastes.

gum ghatti a **gum** from the tree *Anogeissus latifolia*. It has a complex structure and contains as major components D-mannose, D-galactose, and L-arabinose, the latter in both furanose and pyranose arrangement. Small amounts of D-xylose and D-glucuronic acid are also present.

Gunn rat any member of a mutant strain of Wistar rats with hereditary hyperbilirubinemia. The defect affects the rate of glucuronidation of a number of substrates, but not equally. [After C. H. Gunn.]

Güntelberg–Müller charging process a method of calculating the electrical energy of an ion. According to the process, only the ion under consideration is supposed to receive a charge; the surrounding ions are assumed to be already charged, and the only change that they undergo during the process is a gradual redistribution as the central ion receives its charge.

Guo *symbol for* a residue of the ribonucleoside guanosine (alternative to G).

Guo*P* *symbol for* guanosine phosphate.

Guo2′*P* *symbol for* guanosine 2′-phosphate; *see* **guanosine phosphate**.

Guo-2′,3′-*P* *symbol for* guanosine 2′,3′-phosphate; *see* **guanosine phosphate**.

Guo3′*P* *symbol for* guanosine 3′-phosphate; *see* **guanosine phosphate**.

Guo-3′,5′-*P* *symbol for* guanosine 3′,5′-phosphate.

Guo5′*P* *symbol for* guanosine 5′-phosphate.

Guo5′*PP* *symbol for* guanosine diphosphate (alternative to ppG).

Guo*PP*[CH$_2$]*P* *symbol for* guanosine 5′-[β,γ-methylene] triphosphate (alternative to p[CH$_2$]ppG).

Guo*PP*Man *symbol for* guanosinediphosphomannose.

Guo*PP*[NH]*P* *symbol for* guanosine 5′-[β,γ-imido]triphosphate (alternative to p[NH]ppG).

Guo5′*PPP* *symbol for* guanosine 5′-triphosphate (alternative to pppG).

Guo5′*PPP*[S] *symbol for* guanosine 5′-γ-thiotriphosphate.

Guo5′*PP*[S] *symbol for* guanosine 5′-β-thiodiphosphate.

gustducin a taste-cell-specific G-protein α subunit closely related to the transducins and comprising 354 amino acids.

gut a term variously used to describe the whole of the alimentary canal or only the intestine, i.e. the part from the stomach to the anus.

gut glucagon *(sometimes) an alternative term for* **enteroglucagon**.

gut hormone *a general, inaccurate, but widely used term for* all the various regulatory peptides of the gut. They are neither confined to the gut, nor are they exclusively hormones.

Guthrie test a microbiological test in which a strain of *Bacillus*

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subtilis that requires phenylalanine for growth is used to test for excessive levels of plasma phenylalanine in conditions such as **phenylketonuria**. [After R. Guthrie (1916–).]

gutta-percha a *trans*-1,4-polyisoprene derived by coagulation of the latex of various Malayan trees of the genus *Palaquium*. It has a lower molecular mass than rubber and is thermoplastic.

GUU a codon in mRNA for L-valine.

g-value a factor expressing the size of the magnetic moment of a paramagnetic chemical species. It specifies the position at which the absorption in electron spin resonance of the paramagnetic species occurs. *See* **electron spin resonance spectroscopy**.

Gy *symbol for* gray.

gynaminic acid *formerly, a name for* a constituent of human milk, now known to be identical with **sialic acid**.

gynogamone *see* **gamone**.

gyrase *see* type II **DNA topoisomerase**.

gyromagnetic ratio *or* **magnetogyric ratio** *symbol*: γ; the ratio of the magnetic moment, μ, of a given atomic particle to its angular momentum, L; i.e. $\gamma = \mu/L$. *See also* **proton magnetogyric ratio**.

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Hh

h *symbol for* **1** hecto+ (SI prefix denoting 10^2 times). **2** hour (supersedes hr.).

h *symbol for* **1** Planck constant. **2** Hill coefficient (alternative to n_H). **3** height.

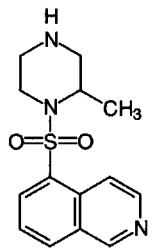
h+ *or (not recommended)* **H+** *prefix* to abbreviations for peptide hormone (names) denoting human, i.e. of (or as if of) human origin; e.g. hGH (for human growth hormone).

H *symbol for* **1** hydrogen; *see also* **protium**, **deuterium**, **tritium**. **2** a residue of the α-amino acid **histidine** (alternative to His). **3** a residue of an incompletely specified base in a nucleic-acid sequence that may be adenine, cytosine, or either thymine (in DNA) or uracil (in RNA). **4** henry. **5** histone. **6** histamine (*see* **histamine receptor**).

H+ *see* **h+**.

H1 a DNA-binding protein from *Escherichia coli* belonging to the **H-NS** family of proteins.

H7 1-(5-isoquinolinylsulfonyl)-2-methylpiperazine; an inhibitor of protein kinase C (K_i = 6.0 μM), protein kinase A (K_i = 3.0 μM), and cyclic GMP-dependent protein kinase (K_i = 5.8 μM).



H_2 *symbol for* **1** dihydrogen. **2** the prefix **dihydro+** in a trivial chemical name, e.g. H_2folate for dihydrofolate.

H_4 *symbol for* the prefix **tetrahydro+** in a trivial chemical name, e.g. H_4folate for tetrahydrofolate.

H *symbol for* **1** fluence (alternative to *F*). **2** enthalpy. **3** magnetic field strength (light italic in nonvector equations; bold italic in vector equations).

-H *conformational descriptor* designating the half-chair conformation of a six-membered ring form of a monosaccharide or monosaccharide derivative. Locants of ring atoms that lie on the side of the structure's reference plane from which the numbering appears clockwise are indicated by left superscripts and those that lie on the other side of the reference plane by right subscripts; e.g. methyl 2,3-anhydro-5-thio-β-L-lyxopyranoside-^5H_S. *See also* **conformation**.

H- *or (sometimes)* ***H*** *(in chemical nomenclature) symbol for* indicated hydrogen (at the position specified by a prefixed locant).

Haber, Fritz (1868–1934), German chemist; Nobel Laureate in Chemistry (1919) 'for the synthesis of ammonia from its elements'.

Haber–Weiss reaction the iron-catalysed reaction of a superoxide anion with hydrogen peroxide to form oxygen, a hydroxyl radical, and a hydroxyl ion. It is thought to proceed as follows:

$$O_2^- + Fe^{3+} \rightarrow O_2 + Fe^{2+}$$

$$H_2O_2 + Fe^{2+} \rightarrow OH^{\bullet} + OH^- + Fe^{3+}$$

[After F. **Haber** and Joseph Weiss.]

HAc *abbr. for* acetic acid.

HACBP *see* **calreticulin**.

haem *a variant spellings (esp. Brit.) of* **heme**.

haema+ *or (before a vowel)* **haem+** *variant spellings (esp. Brit.) of* **hema+**.

haemadin an anticoagulant peptide from the Indian leech, *Haemadipsa sylvestris*. It is a slow tight-binding inhibitor of thrombin, but does not inhibit trypsin, chymotrypsin, factor Xa, or plasmin. It comprises 57 amino acids.

haemato+ *or (before a vowel)* **haemat+** *variant spellings of (esp. Brit.) of* **hemato+**.

haemo+ *a variant spelling (esp. Brit.) of* **hemo+**.

haemoglobin *a variant spelling (esp. Brit.) of* **hemoglobin**.

Hageman factor *an alternative name for* factor XII; *see* **blood coagulation**.

hairpin any part of a linear molecular structure, e.g. of a polynucleotide strand or a prostaglandin, in which two adjacent segments of the molecule are folded back one on the other and held in that conformation by secondary molecular forces such as hydrogen bonds or van der Waals interactions. **Hairpin DNA** (*or* foldback DNA *or* loopback DNA) contains **inverted repeats**; when denatured it renatures extremely rapidly by concentration-independent intrachain base-pairing between complementary sequences of the inverted repeat. Similar structures occur in certain large RNA molecules. The hairpin conformation of a prostaglandin molecule is thought to be necessary for expression of its hormonal activity; in this conformation the α and κ chains of each molecule are extended, parallel to one another, at van der Waals contact distance for their full lengths. *See also* **ribozyme**, **beta bend**.

Haldane coefficient the difference, per bound dioxygen molecule, in the number of hydrons bound by oxy- and deoxyhemoglobin, at constant pH. [After John Scott Haldane (1860–1936), British physiologist.]

Haldane effect the observation that oxygenated blood absorbs less carbon dioxide than deoxygenated blood. It is the reciprocal of the **Bohr effect**.

Haldane gas-analysis apparatus an apparatus once used for the estimation of the carbon dioxide and dioxygen contents of a gas sample.

Haldane relation a relation for reversible enzyme reactions. In the single-substrate, essentially reversible reaction:

$$E + S \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} ES \underset{k_{-2}}{\overset{k_2}{\rightleftharpoons}} EP \underset{k_{-3}}{\overset{k_3}{\rightleftharpoons}} E + P$$

the overall equilibrium constant,

$$K = C_P/C_S = k_1k_2k_3/k_{-1}k_{-2}k_{-3},$$

where C_S and C_P are the concentrations of substrate, S, and product, P, respectively. It can further be shown that

$$K = V_SK_{mP}/V_PK_{mS},$$

where V_S and V_P are the maximum velocities of the reactions S → P in the absence of P and of P → S in the absence of S, and K_{mS} and K_{mP} are the respective Michaelis constants for these reactions. [After John Burdon Sanderson Haldane (1892–1964), British biochemist, physiologist, and geneticist]

half-boat conformation either of the **conformations** of a nonplanar monounsaturated six-membered ring compound when the two ring atoms not directly bound to the doubly bonded atoms lie on the same side of the plane containing the other four (adjacent) atoms.

half-cell one half of an **electric cell**, consisting of one reversible electrode inserted into a solution. Electrical connection between this solution and that in another half-cell is required to complete the electric circuit.

half-chair conformation **1** either of the **conformations** of a nonplanar monounsaturated six-membered ring compound when the two ring atoms not directly bound to the doubly bonded atoms lie on opposite sides of the plane containing the

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other four (adjacent) atoms. **2** any conformation of the six-membered ring form of a monosaccharide or monosaccharide derivative when four adjacent ring atoms are coplanar and the other two lie on opposite sides of the plane. The conformational descriptor *-H* may be added to the name of such compounds.

half-cystine *or* **hemicystine** *symbol*: $_{Cys}^{|}$ *or* $^{Cys}_{|}$; the group formally derived by removal of a hydrogen atom from the thiol group on the side chain in cysteine (or a cysteine residue), or by homolysis of the dithio linkage in cystine (or a cystine residue). It is used in describing or depicting the content or the linear sequence of amino-acid residues in a polypeptide when it contains more than two apparent cysteine residues and the positions of any dithio linkages between them are not known, or when only a coded sequence is being considered.

half-cystyl *or* **hemicystyl** the acyl group, ·S–CH_2–$CH(NH_2)$–CO–, derived from the **half-cystine** group. *Compare* **cysteinyl**.

half-ester any monoester of a dibasic acid.

half-life **1** *symbol*: $t_{½}$ *or* $T_{½}$; the time for one half of the atoms of an amount of radionuclide to undergo radioactive decay. **2** a similar measure of the stability (i.e. rate of decay) of an excited atom or molecule, a radical, an unstable elementary particle, etc. **3** the time for one half of the amount of an administered substance to be metabolized or excreted. If the substance is radioactive, the time required for one half of the dose to be eliminated biochemically or physiologically is termed the **biological half-life** and that required for one half to disappear by radioactive decay as well as by the elimination is the **effective half-life**. **4** *or (sometimes)* **half-time** *symbol*: $t_{½}$; the time required for the concentration of a reactant in a chemical reaction to reach a value that is the arithmetic mean of its initial and final (equilibrium) values. **5** the time for one half of the number of cells in a tissue or organ to be replaced by new cells.

half-of-the-sites reactivity *or* **half-site reactivity** a phenomenon shown by many enzymes that exhibit **negative cooperativity**, in which the maximal stoichiometric yield of either an enzyme–substrate intermediate or a product in a single turnover amounts to only half the number of apparently equivalent active sites. This may be caused by the binding of substrate to one site of a dimeric enzyme, e.g., inducing a conformational change in the enzyme so as to abolish completely the binding affinity of the other site.

half-reaction either of the two coupled chemical changes that together constitute an oxidation–reduction reaction. In one half-reaction there is a gain of electrons and in the other half-reaction a corresponding loss of electrons.

half-site reactivity *an alternative name for* **half-of-the-sites reactivity**.

half-thickness the thickness of a piece of a specified material that will reduce the intensity of a beam of transmitted electromagnetic radiation to one half that of the incident beam.

half-time *an alternative name for* **half-life** (def. 4) for a first-order process.

half-time of exchange the time taken for one half of the exchangeable atoms (or molecules) to be exchanged in a reaction involving such an exchange.

half-wave potential the electrical potential at the mid-point of the current–voltage curve in **polarography**.

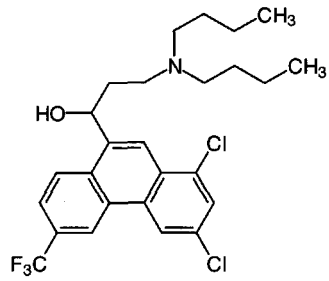
halide *or* **halogenide** **1** an anion of any halogen. **2** a salt of any halogen acid (halogen hydride). **3** any compound containing halogen atoms in organic linkage.

hallucinogen any drug or other substance that causes hallucinations. —**hallucinogenic** *adj.*

halo+ *or (sometimes before a vowel)* **hal+** *comb. form* **1** relating to or containing a halogen. **2** relating to the sea or salt.

halochromism the phenomenon or property of the formation of strongly coloured compounds on the addition of strong acids or certain metallic salts to colourless or faintly coloured substances.

halofantrine 1,3-dichloro-α-[2-(dibutylamino)-ethyl]-6-(trifluoromethyl)-9-phenanthrenemethanol; a derivative of 9-phenanthrenemethanol that is effective against chloroquine-resistant malarial infections.

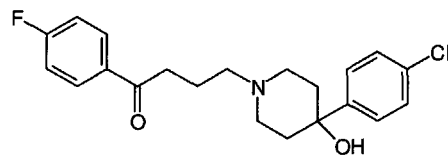


halogen any of the monovalent chemical elements of group 17 of the IUPAC **periodic table**: fluorine, chlorine, bromine, iodine, and astatine.

halogenate to treat or react (a substance) with a halogen; to introduce one or more halo groups into an organic compound. —**halogenation** *n.*

halogenide *an alternative name for* **halide**.

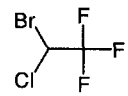
haloperidol 4-[4-(4-chlorophenyl)-4-hydroxy-1-piperidinyl]-1-(4-fluorophenyl)-1-butanone; one of the butyrophenone group of **neuroleptic** drugs.



halophile **1** an organism that grows in or tolerates saline conditions, especially concentrations of sodium chloride equal to or greater than that in sea water. **2** describing such an organism. —**halophilic** *adj.*

halorhodopsin an energy-transducing pigment identified in membranes of *Halobacterium halobium*. It is similar to, but distinct from **bacteriorhodopsin** and is associated with a light-driven pump for sodium ions.

halothane *the trivial name for* 2-bromo-2-chloro-1,1,1-trifluoroethane, a widely used, volatile, lipid-soluble general inhalational anesthetic agent.



hamamelose 2-*C*-(hydroxymethyl)-D-ribose; a substance found principally in **tannin** of witch hazel (*Hamamelis virginiana*).

Hamburger shift *an alternative name for* **chloride shift**.

Hamiltonian operator *symbol*: H; a function used to express the total energy of a system in joules: $H = T + V$, where T is the kinetic energy operator and V the potential energy operator. For a particle of mass m and momentum $\boldsymbol{p}$,

$$H = \boldsymbol{p}^2/2m + V.$$

[After William Rowan Hamilton (1805–65), Irish astronomer and mathematician.]

hammerhead *see* **ribozyme**.

handedness a form of terminology (based on the human left and right hands) for describing objects and compounds that

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are mirror images of each other and hence nonsuperimposable. A pair of **enantiomers** display molecular handedness. *See* **chirality**.

handle *a colloquial term for* any chemical group attached to a specified substance with the purpose of making it more easily identified, more reactive, or more easily operated upon, or one that may serve in targeting or specific binding. The attachment of a handle may be brought about chemically or metabolically.

handle technique a technique used to separate excess alkylating agents from products in peptide synthesis. For instance, the C terminus of a growing peptide chain can be protected with a basic function, e.g. by forming a 4-picolyl ester of the carboxyl group, thereby allowing separation of the products on cation-exchange resin columns or by extraction into aqueous acidic solutions.

Hanes plot a graphical method for treating enzyme kinetic data using the following form of the Michaelis equation (*see* **Michaelis kinetics**):

$$s/v = K_m/V + s/V$$

where s is the substrate concentration, v is the velocity of the reaction, and V is the limiting rate. If s/v is plotted against s, the slope of the resulting straight line is $1/V$, the intercept on the s/v axis is K_m/V, and the intercept on the s axis is $-K_m$. [After Charles Samuel Hanes (1903–90), British biochemist.]

Hanks' balanced salt solution *abbr.*: HBSS; a balanced salt solution used in tissue culture to provide a suitable ionic and osmotic environment for cell growth and development. It contains, per 100 mL of distilled water, 0.8 g NaCl, 0.04 g KCl, 0.01855 g $CaCl_2 \cdot 1H_2O$, 0.02 g $MgSO_4 \cdot 7H_2O$, 0.006 g KH_2PO_4, 0.00475 g Na_2HPO_4, 0.0350 g $NaHCO_3$, 0.1 g glucose, and 0.0017 g sodium Phenol Red. The pH is 7.0–7.2.

Hansch equation an equation relating the differences in the partitions of variously substituted compounds between an organic and an aqueous phase to the **hydrophobicity constant**, π, of the substituent. If P_0 is the ratio of the solubility of the parent compound in an organic phase to that in the aqueous phase, and P is the corresponding ratio for the substituted compound, then: $\pi = \log(P/P_0)$.

Hansenula *see* **methylotrophic yeasts**.

H antigen *see* **blood-group substance**.

haploid describing a cell, an organism or a nucleus of a cell having a single genome or a single set of homologous chromosomes; i.e. containing half the **diploid** number; having a **ploidy** of one. —**haploidy** *n*.

haplotype a set of genes located on a single chromosome; the term is used also to denote the characteristics dependent on those genes. In outbred populations the maternal and paternal chromosomes usually differ, so an individual has two haplotypes, one derived from each parent.

'happiness hormone' *a jocular name for* any **endorphin** or **enkephalin**, so-named because of the supposed ability of such substances to promote a sense of well-being.

hapt+ *a variant form of* **hapto+** (before a vowel).

hapten any, usually small, substance that can combine specifically with antibody but that is not immunogenic unless bound to a **carrier** (def. 8). Most haptens carry only one or two antigenic determinants. —**haptenic** *adj.*

hapten-inhibition test a serological test for characterizing an antigenic determinant. It involves the use of haptens of known structure to block the combining site of a particular antibody.

hapten-sandwich labelling a variant of the **sandwich technique** for amplification of an antigen–antibody reaction. In this modification, the primary antibody, specific for the antigen of interest, is combined with a number of residues of a hapten, e.g. *p*-azobenzene arsonate. The secondary (labelled or marked) antibody is a specific anti-hapten antibody; on reaction of secondary antibody molecules with a molecule of primary antibody, the hapten residues become sandwiched between the large molecules of antibody. By the use of different haptens and two or more non-cross-reactive anti-hapten antibodies bearing distinguishable markers, two or more antigens on the same or different cells may simultaneously be labelled.

hapticity *symbol*: η; the attribute of a ligand entity or group that combines with a central (usually metal) atom to form a coordination entity in which the central atom is bonded to two or more contiguous atoms of the ligand rather than to a specific atom. Such a coordination entity is frequently (but not exclusively) a **pi adduct**. *See also* **hapto**.

hapto *or (less commonly)* **eta** *(in chemical nomenclature)* the name by which to read the symbol η- (Greek eta), when prefixed to the name of the ligand group in a coordination entity (with added locants if appropriate) to indicate hapticity.

hapto+ *or (before a vowel)* **hapt+** *comb. form* indicating ability to bind or combine.

haptocorrin a blood cobalamin-binding glycoprotein that may prevent uptake of bacterial cobalamin analogues. Example from *Sus scrofa* (fragment): database code HAPC_PIG, 416 amino acids (46.91 kDa).

haptoglobin *abbr.*: Hp; any α_2 globulin of blood plasma that can combine with free oxyhemoglobin to form a stable, ≈300 kDa, complex. Such combinations occur when hemoglobin is liberated in the blood, and the complexes so formed, which have weak peroxidase activity and cannot be filtered by the kidney, are rapidly removed and degraded in the tissues. Three human haptoglobin phenotypes are known, designated Hp 1-1, Hp 2-2, and Hp 2-1, each of which contains two pairs of nonidentical polypeptide chains, α and β, joined by disulfide bonds. There are two kinds of α chain, α_1 of 84 amino-acid residues (9 kDa) and α_2 of 143 residues (17 kDa), and a single kind of β chain, of 244 residues (in human). The α_2 chain, found solely in human haptoglobin, is identical in sequence to that of residues 1–71 or 1–72 of an α_1 chain linked to residues 11 or 12 to 84. The basic subunit structure of Hp 1-1 is $(\alpha_1\beta)_2$, that of Hp 2-2, $(\alpha_2\beta)_2$, and that of Hp 2-1, $(\alpha_2\beta)(\alpha_1\beta)$. However, the α_2 chain has an odd number of half-cystine residues, as a consequence of which larger oligomers of Hp 2-2 and Hp 2-1 may arise by formation of disulfide bonds with α_2 chains of other molecules or of $(\alpha_2\beta)$ half-molecules. Example (precursor) from human: database code HPT1_HUMAN, 347 amino acids (38.45 kDa).

haptomer any substance (such as a lectin or the B fragment of diphtheria toxin) that can interact with the cell membrane and that binds or can be bound to an **effectomer** (such as gelonin or the A fragment of diphtheria toxin), thereby allowing the effectomer to exert its toxic action on intact cells. —**haptomeric** *adj.*

haptophore a term introduced by Ehrlich to denote the specific chemical group in a toxin (i.e. antigen) molecule that attaches it to an antitoxin (i.e. antibody) molecule. Unlike the **toxophore**, it is not destroyed on conversion of the toxin to a toxoid.

H^+(aq) *symbol for* the hydrated hydrogen ion, the normal state of the hydrogen ion in aqueous solutions, consisting of a hydron surrounded by a shell of water molecules held by ion–dipole interaction. *Compare* **oxonium** (def. 1).

hard *(in radiation physics)* describing corpuscular or electromagnetic ionizing radiation (especially beta particles or X- or gamma-radiation) having relatively high energy, hence high ionizing power and long-range or high penetrating power. Hard X- or gamma-radiation has short wavelengths. *Compare* **soft** (def. 1).

Harden, (Sir) Arthur (1865–1940), British chemist and biochemist distinguished for his discoveries (with W. J. Young) that fermentation of sugar by yeast juice involved a heat-stable and separable fraction (later named cozymase by H. von Euler), required the presence of phosphate, and (also with R. Robison) resulted in the intermediate formation of two hexose phosphates (*see* **Harden–Young ester**, **Robison ester**); Nobel Laureate in Chemistry (1929), the prize being shared with H. von Euler 'for their investigations on the fermentation of sugar and fermentative enzymes'.

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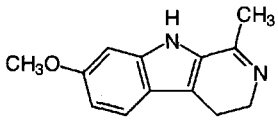
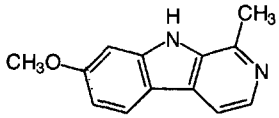
Harden–Young ester *a former name for* D-fructose 1,6-bisphosphate (before its chemical structure had been elucidated). [After A. **Harden** and William John Young (1878–1942), British biochemists.]

Hardy–Weinberg law a mathematical statement about the relation between gene frequencies and genotype frequencies within a population. If the genotypes are AA, Aa, and aa, and p is the frequency of allele A in the population, and q the frequency of allele a, so that $p + q = 1$, then the relative proportions of the three genotypes in the population, AA:Aa:aa, is given by $p^2:2pq:q^2$. [After Godfrey Harold Hardy (1877–1947), British mathematician, and Wilhelm Weinberg (1862–1937), German physician.]

harmaline 4,9-dihydro-7-methoxy-1-methyl-3*H*-pyrido[3,4-*b*]indole; dihydroharmine; a cardioactive alkaloid from Syrian rue, *Peganum harmala* that also has hallucinogenic properties. *See also* **harmine**.



harmine 7-methoxy-1-methyl-9*H*-pyrido[3,4-*b*]indole; a β-carboline alkaloid found in, e.g., *Peganum harmala* (Syrian rue). It inhibits monoamine oxidase and is a central nervous system stimulant. *See also* **harmaline**.



HART *abbr. for* hybrid-arrested translation.

Hartley filter funnel a development of the **Büchner funnel** comprising three pieces, the reservoir, a perforated plate to support the filter disk, and a conical piece to collect the filtrate. [After (Sir) Percival Hartley (1881–1957), British bacteriologist.]

Hartline, Haldan Keffer (1903–83), US neurophysiologist; Nobel Laureate in Physiology or Medicine (1967) jointly with R. Granit and G. Wald 'for their discoveries concerning the primary physiological and chemical visual processes in the eye'.

Hartnup disease a rare, autosomal recessively inherited condition of humans in which there is a specific hyperaminoaciduria and indoluria, due to a diminished capacity for renal reabsorption of a group of monoamino-monocarboxylic acids, especially tryptophan. There may also be an impaired transport of the same group of amino acids across the gut wall. The aminoaciduria is often associated with a pellagra-like skin rash, due to inefficient tryptophan utilization and metabolism. The pellagra may often be resolved by oral nicotinic acid. The primary defect remains unknown. [After E. Hartnup, the first patient with the condition to be described.]

hashish a resinous extract obtained from the dried flower tops of the hemp plant (*Cannabis sativa*). The term may sometimes be used for various other extracts. *See* **cannabis**.

Hassel, Odd (1897–1981), Norwegian physical chemist; Nobel Laureate in Chemistry (1969), the prize being shared with D. H. R. Barton 'for their contributions to the development of the concept of conformation and its application in chemistry'.

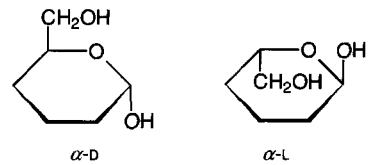
HAT *abbr. for* hypoxanthine-aminopterin-thymidine (medium); a selective medium used in tissue culture. It is of particular use in the production of **hybridomas**. The medium was originally devised to select against cells deficient in hypoxanthine-guanine phosphoribosyltransferase (HGPRT⁻ cells). Amethopterin blocks *de novo* synthesis of purines and HGPRT⁻ cells are unable to utilize the salvage pathway, and hence are killed.

hatching enzyme *see* **envelysin**.

Hatch–Slack pathway *or* **C_4 cycle** *or* **C_4 pathway** a metabolic pathway for carbon-dioxide translocation occurring in **C_4 plants**. In the mesophyll cells **phospho*enol*pyruvate carboxylase** catalyses the condensation of CO_2 with phospho*enol*pyruvate to form oxaloacetate; this is then reduced to malate by light-generated NADPH. The malate passes into the bundle-sheath cells where it is oxidatively decarboxylated by the **malic enzyme** to pyruvate and CO_2; the pyruvate returns to the mesophyll cells and is reconverted to phospho*enol*pyruvate by ATP and pyruvate dikinase; the CO_2 remains in the bundle-sheath cells where it enters the **reductive pentose phosphate cycle**. The overall effect of the pathway is to carry CO_2 from the mesophyll cells, which are in contact with air, to the bundle-sheath cells, which are the major sites of photosynthesis.

Haworth, (Sir) Walter Norman (1883–1950), British organic chemist noted for his structural studies on monosaccharides (*see also* **Haworth representation**) and polysaccharides and for producing the first chemical synthesis of ascorbic acid, vitamin C; Nobel Laureate in Chemistry (1937) 'for his investigations on carbohydrates and vitamin C' [prize shared with P. Karrer].

Haworth representation a diagrammatic way of unambiguously representing the structural formulae of the cyclic forms of monosaccharides to show on a plane surface the relative configurational arrangements of the atoms and groups in space. Pyranoses are represented by a hexagon (five carbons and one oxygen) and furanoses by a pentagon (four carbons and one oxygen). A Haworth representation is derived from a **Fischer projection** as follows. The monosaccharide in question is depicted with the carbon-chain horizontal and in the plane of the paper, the potential carbonyl group being to the right. The oxygen bridge is then depicted as being formed behind the plane of the paper. The heterocyclic ring is therefore located in a plane approximately perpendicular to the plane of the paper and the groups attached to the carbon atoms of that ring are above and below the ring. The edge of the ring nearer the viewer is indicated by thickened lines. For clarity, the carbon atoms of the ring and their attached hydrogen atoms are not shown. Groups that, in the Fischer projection, appear to the right of the vertical chain then appear in the Haworth representation below the plane of the ring. However, at the asymmetric carbon atom involved via oxygen in ring formation



(e.g. C-5 in glucopyranose, C-4 in glucofuranose), a rotation about the bond to the preceding carbon atom must be envisaged in order to bring that oxygen atom into the correct orientation to link to the carbon atom of the carbonyl group. Thus, if the hydroxyl group that is engaged in ring formation lies to the right in the Fischer projection, the group that lies below it must point upwards in the Haworth representation, whereas if it lies to the left, it must point down in the Haworth representation. In representing the α and β anomers in the Haworth convention, it should be noted that for the α anomer, the anomeric hydroxyl points in the opposite direction to the R group (see structure); for D-sugars, the R group points upwards, so the α-hydroxyl must point down; conversely, if the R group points down (as in α-L-glucose), the α anomeric hydroxyl must point upwards. The above rules only obtain if the

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ring is numbered clockwise from the anomeric carbon, as is frequently the case, and it is important to appreciate that Haworth representations, unlike Fischer projections, cannot be rotated in the plane of the paper but must be reorientated in space.

Hb *abbr. and symbol for* hemoglobin; hence, e.g., HbO_2 symbolizes oxyhemoglobin, and HbCO symbolizes carbonmonoxyhemoglobin.

Hb A *abbr. for* adult hemoglobin.

H band *an alternative name for* H zone (*see* **sarcomere**).

HBD *(in clinical chemistry) abbr. for* α-hydroxybutyrate dehydrogenase, the LD_1 isoenzyme of **lactate dehydrogenase**, or 'heart-specific' lactate dehydrogenase, which is assayed using 2-hydroxybutanoate as substrate, a substance that does not occur naturally.

Hb F *abbr. for* fetal hemoglobin.

Hb S *abbr. for* sickle-cell hemoglobin; *see* **sickle cell**.

HBSS *abbr. for* Hanks' balanced salt solution.

hCG *or* **HCG** *abbr. for* human choriogonadotropin (*see* **choriogonadotropin**).

H chain *see* **heavy chain**.

HCO *symbol for* the formyl group (alternative to For).

HCR *abbr. for* host-cell reactivation.

Hcy *symbol for* a residue of the α-amino acid L-homocysteine.

HDEL a four-residue motif, His-Asp-Glu-Leu, of similar function to the **KDEL** motif.

HDH *abbr. for* **histidinol dehydrogenase**.

HDL *abbr. for* high-density lipoprotein.

HDP *abbr. for* helix-destabilizing protein.

He *symbol for* helium.

head **1** the foremost or uppermost part of the body of an animal; in vertebrates it comprises the skull containing the mouth, brain, and the organs of hearing, sight, smell, and taste. **2** the part of a molecular structure that bears a specific functional group or that is polar, reactive, bulky, or in some other characteristic way differs from the remainder of the molecule. **3** *a common name for* a centrifuge rotor.

headgroup of a polar lipid, that part of the molecule that expresses its polar character. For a phospholipid, this comprises the phosphate group together with any polar entity attached to it. For a glycolipid, it comprises the carbohydrate moiety.

headspace analysis a technique used in the identification of microorganisms involving gas-chromatographic analysis of the vapour in the headspace above the specimen or culture.

heat *symbol*: q or Q; the energy possessed by a system in the form of kinetic energy of atomic or molecular translation, rotation, or vibration. It is measured in joules or calories. Heat energy can be transferred from points of higher temperature to points of lower temperature by conduction, convection, or radiation. When the temperature of a system changes, its enthalpy (heat content) changes by an amount equal to the product of its mass, specific heat capacity, and its change in temperature.

heat capacity *symbol*: C; the amount of heat required to raise the temperature of a body or a system by 1 kelvin; it is usually measured in joules per kelvin. The **heat capacity at constant pressure**, C_p, is given by: $C_p = (\partial H/\partial T)_p$ J K^{-1} and the **heat capacity at constant volume**, C_v, is given by: $C_v = (\partial U/\partial T)_v$ J K^{-1} where H is the enthalpy, U the internal energy, and T the thermodynamic temperature.

heat content *another name for* **enthalpy**.

heat-labile *describing molecules that decompose at elevated* temperatures or that lose biological activity when heated to a moderate temperature, e.g. 50 °C.

heat of activation the difference in heat content between a transition state and the state of its reactants.

heat of combustion the amount of heat evolved when a given amount, usually one mole, of a substance is completely burnt in dioxygen.

heat of evaporation *an alternative name for* **heat of vaporization**.

heat of formation the amount of heat absorbed or evolved when one mole of a substance is formed from its elements.

heat of fusion *or* **heat of melting** the amount of heat absorbed or evolved when a specified quantity of substance, usually one mole, is converted from the solid to the liquid state at a specified pressure and a specified temperature. If the pressure is 1 atm the temperature is the melting point of the substance.

heat of neutralization the amount of heat absorbed or evolved when one mole of an acid or base is completely neutralized.

heat of reaction the amount of heat absorbed or evolved in the course of a (bio)chemical reaction, usually expressed per mole of reacting substances.

heat of solution the amount of heat absorbed or evolved when one mole of a substance is dissolved in a large volume of specified solvent.

heat of vaporization *or* **heat of evaporation** the amount of heat absorbed or evolved when a specified amount of substance, usually 1 mole, is converted from the liquid to the vapour state at a specified pressure and a specified temperature. If the pressure is 1 atm the temperature is the boiling point.

heat-shock protein *abbr.*: hsp; any of a group of specific proteins that are synthesized by both prokaryotic and eukaryotic cells, e.g. bacteria, yeasts, and *Drosophila*, after they have been exposed to a temperature that is higher than normal. Other stresses, such as free-radical damage, have a similar effect. Many members of the hsp family are not induced but are normally present in all cells. Human cells in culture also produce heat-shock proteins but the induction of heat-shock proteins has not been clearly demonstrated in the human body. The heat-shock proteins are classified, according to their size, in three classes, Hsp60, Hsp70, and Hsp90. They are characterized by their role as molecular **chaperones**. A major chaperone in the lumen of the endoplasmic reticulum is **binding protein**, a member of the Hsp70 class. These proteins are highly conserved in structure so that the proteins from *Escherichia coli* and human are 50% identical in primary structure. The Hsp70 proteins possess ATPase and peptide binding domains. The other members of the Hsp70 class are Grp75 in mitochondria and **DnaK** in bacterial cytosol. In the Hsp60 class is GroEL in bacterial cytosol (*see* ***groEL***). Example, hsp71: database code HS71_HUMAN, 641 amino acids (69.97 kDa).

heat-shock regulatory element *or* **heat-shock response element** *abbr.*: HSE; a base sequence in prokaryotic and eukaryotic genomes responsible for regulating gene expression in response to heat-shock and related stress situations.

heat-shock response element *see* **HSE**.

heat-stable describing something that retains its (bio)chemical activity when heated to a moderate temperature, e.g. 50 °C.

heavy *(in physics)* of more than the usual mass. *Compare* **light** (def. 2).

heavy atom *or* **heavy isotope** *or* **heavy nuclide** an isotopic form of an atom that contains more than the common number of neutrons and is thus of greater relative atomic mass than the most abundant or most commonly observed isotope.

heavy carbon *see* **carbon-13**.

heavy chain *or* **H chain** the heavier of the two types of polypeptide chain found in **immunoglobulin** molecules. Each heavy chain is linked, usually by disulfide bonds, to a **light chain** and to another, identical heavy chain. Heavy chains differ in relative molecular mass according to the type of immunoglobulin: in humans the M_r is ≈50 000 in IgG and ≈70 000 in IgM. Each heavy chain consists of an **Fc fragment** and an **Fd fragment**. Heavy chains carry the antigenic determinants that differentiate the various immunoglobulin classes.

heavy-chain disease a rare disease of humans in which there are tumours of lymphoid tissue associated with the presence of free immunoglobulin fragments in plasma and urine.

heavy-chain switch *or* **H-chain switch** the change in the expression of the immunoglobulin **heavy chain** (H chain) gene system as manifested by the predominance of IgM (μ chain class) in the primary immune response and by the predominance of IgG_1 (γ chain class) in the **secondary immune response**.

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heavy hydrogen *an alternative name for* **deuterium**.

heavy meromyosin *abbr.*: H-meromyosin *or* HMM; a 350 kDa fragment produced when **myosin** is subjected to tryptic digestion. It contains part of the helical, rod-shaped tail and both the attached globular heads of the original myosin molecule. Heavy meromyosin retains both the ATPase and the actin-binding activity of myosin.

heavy nitrogen the stable nuclide $^{15}_{7}N$ (nitrogen-15); relative abundance in natural nitrogen 0.37 atom percent. It is used as a tracer in studies of nitrogen metabolism.

heavy oxygen the stable nuclide $^{18}_{8}O$ (oxygen-18), usually accompanied by the stable nuclide $^{17}_{8}O$ (oxygen-17); relative abundances in natural oxygen: $^{18}_{8}O$, 0.20 atom percent; $^{17}_{8}O$, 0.037 atom percent. $^{18}_{8}O$ is used as a tracer in studies of reaction mechanisms and of oxygen metabolism.

heavy strand *or* **H strand** **1** any polynucleotide chain labelled with a heavy isotope, e.g. nitrogen-15. **2** any naturally occurring chain in a polynucleotide duplex that is heavier or has a greater density than the complementary strand.

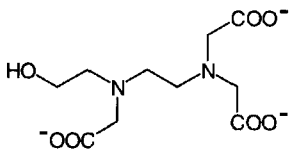
heavy water deuterium oxide; *symbol*: $^{2}H_2O$ *or* D_2O; water in which the hydrogen atoms in all of the molecules have been replaced by deuterium; or water in which the hydrogen is appreciably enriched in deuterium. The M_r of pure $^{2}H_2O$ is 20.028. Heavy water is prepared from natural water by exchange techniques or by fractional distillation or electrolysis. It is used as a tracer in metabolic studies, in investigation of reaction mechanisms, and as a solvent in resonance spectroscopy.

hect+ *see* **hecto+** (def. 2).

hecto+ **1** *symbol*: h; an SI prefix denoting 10^2 times. **2** *or (before a vowel)* **hect+** denoting 100 or 100 times.

hedgehog protein a transmembrane protein involved in segment polarity and cell-to-cell signalling during embryogenesis and metamorphosis in *Drosophila melanogaster*. Database code (precursor): HH_DROME, 471 amino acids (52.03 kDa). *See also* **sonic hedgehog protein**.

HEDTA *abbr. for* *N*-(2-hydroxyethyl)ethylenediamine triacetate, or its trisodium salt, or for its partially or fully protonated forms. It is a chelating agent, especially for ferric ions in the pH range 7.0–10.0.



HEETP *abbr. for* height equivalent to an effective theoretical plate.

Heidelberger, Michael (1888–1991), US pathologist described as the father of modern immunology. The recipient of numerous awards, he continued to carry out research almost to the end of his life at age 103.

height equivalent to an effective theoretical plate *abbr.*: HEETP; *symbol*: *H*; *(in chromatography)* the column length divided by the **effective theoretical plate number**.

height equivalent to a theoretical plate *or* **plate height** *abbr.*: HETP; *symbol*: *h*; *(in chromatography)* the column length divided by the **theoretical plate** number.

Heisenberg, Werner Karl (1901–76), German theoretical physicist renowned for his work on quantum theory and atomic structure and for advancing (in 1927) the theory known later as the **Heisenberg uncertainty principle**; Nobel Laureate in Physics (1932) 'for the creation of quantum mechanics', the application of which has, *inter alia*, led to the discovery of the allotropic forms of hydrogen'.

Heisenberg uncertainty principle the principle that the simultaneous precise determination of the velocity (or any related property, e.g. momentum or energy) of a material particle and its position is impossible; the smaller the particle the greater the degree of uncertainty. [After Werner Karl Heisenberg (1901–76), German physicist; Nobel Laureate in Physics (1932).]

HeLa cell an established tissue culture strain of human epidermoid carcinoma cells containing 70–80 chromosomes per cell (compared with 46 in normal cells). It is much used for biochemical work. HeLa cells have been in continuous culture since 8 February 1951, and were derived from tissue removed from a patient named Henrietta Lacks.

helical cross *a name sometimes given to* the X-shaped pattern of X-ray scattering from a continuous helical molecule.

helicase *a name sometimes given to* the protein (**repA**) that promotes the ATP-dependent unwinding of the parental DNA duplex during DNA replication. *See also* **DNA helicase**, **RNA helicase**.

helicorubin a *b*-type cytochrome that occurs in the hepatopancreas of the snail *Helix pomatia* and related species.

helix (*pl.* **helices**) **1** a coiled or spiral structure, e.g. the thread of a bolt or a coil (tubular) spring. *See also* **alpha helix**, **beta helix**, **gamma helix**. **2** the curve traced on the surface of a cylinder or cone by a point crossing its right sections at a constant angle. **3** a space curve with turns of constant angle to the base and constant distance from the axis. —**helical** *adj.*; **helicity** *n.*

helix breaker any amino-acid residue that, whenever it occurs in a polypeptide chain, interrupts the α-helical structure; e.g. proline, hydroxyproline, and, sometimes, other residues.

helix-destabilizing protein *abbr.*: HDP; any of a group of proteins that bind tightly and preferentially to single-stranded DNA. They have, theoretically, the following properties: (1) they lower the melting temperature, T_m, for thermally induced **helix-to-coil transition**; (2) they lower the optimum temperature for duplex renaturation; (3) they sterically hinder base pairing and the degradation of single strands by nucleases; (4) they induce a conformation for the single-stranded DNA that is optimal for its function in some processes, e.g. as a template in replication; and (5) they interact with other proteins (enzymes) to potentiate some process involving single-stranded DNA and these proteins.

helix former any amino-acid residue that, whenever it is present in a polypeptide chain, tends to promote an α-helical structure. *Compare* **helix breaker**.

helix-loop-helix *abbr.*: HLH; *an alternative term for* **helix-turn-helix**.

helix-to-coil transition the transition of a macromolecule (polypeptide or polynucleotide) from an ordered to a disordered structure; it is equivalent to **denaturation**. Helix-to-coil transitions are usually detected by monitoring a change in some physical property of the macromolecule such as intrinsic viscosity, optical absorbance, or sedimentation coefficient. *See also* **melting temperature**.

helix-turn-helix (*abbr.*: HTH) *or* **helix-loop-helix** (*abbr.*: HLH) a protein structural feature consisting of two helices separated by a short **beta turn**. It is found in several DNA-binding regulatory proteins; there are two sequence motifs.

helix winding number *see* **supercoil**.

helodermin *see* **exendin**.

helospectin I *see* **exendin**.

helper cell *abbr.*: T_H cell; a **T lymphocyte**, carrying the surface markers CD4 and CD5 in the human (L3T4 and Ly1 in the mouse), that acts as an inducer of the effector cells for both **humoral** and **cell-mediated immunity**. Helper cells recognize and bind to antigen in combination with class II **major histocompatibility complex** molecules on the surface of antigen-presenting cells, and generate lymphokines that stimulate effector cytotoxic cells and B cells. Other cells of the helper phenotype, e.g. $CD4^+$ cells, are known as T-**suppressor** cells and are responsible for suppression, exerting negative feedback control on the helper cells.

helper peak-1 *abbr.*: HP-1; *a former name for* **interleukin 1**.

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helper virus any virus that supplies one or more of the functions that a **defective virus** is unable to perform. When a cell is infected with both a defective virus and a helper virus, the former is able to replicate, a property that can be exploited in various molecular biological techniques.

hem+ *or (esp. Brit.)* **haem+** *a variant form of* **hemo+** (before a vowel).

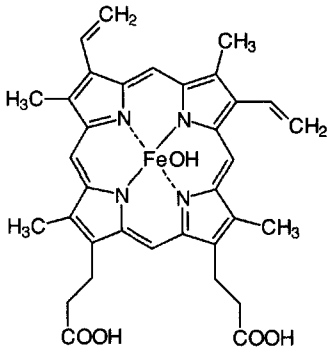
hema+ *or (esp. Brit.)* **haema+** *a variant form of* **hemo+**.

hemagglutination *or (esp. Brit.)* **haemagglutination** the agglutination of red blood cells.

hemagglutinin *or (esp. Brit.)* **haemagglutinin** **1** any **agglutinin** of red blood cells. **2** any nonantibody substance, e.g. a lectin or a surface component of some virus particles, that can agglutinate red blood cells. **3** a viral envelope glycoprotein responsible for the attachment of virus to cell receptors and the initiation of infection. Example from influenza A virus (strain A/Aichi/2/68) (precursor): database code HEMA_IAAIC, 566 amino acids (63.34 kDa); 3-D structure known (much β structure).

hemat+ *or (esp. Brit.)* **haemat+** *a variant form of* **hemato+** (before a vowel).

hematin *or (esp. Brit.)* **haematin** **1** *or* **ferriheme hydroxide** *the trivial name for* ferriprotoporphyrin hydroxide (*formerly called* ferriprotoporphyrin IX hydroxide); hydroxo(protoporphyrinato)iron(III); hydroxoiron(III) protoporphyrinate. *Compare* **heme** (def. 1), **hemin** (def. 1). **2** *the generic name for* any hydroxo(porphyrinato)iron(III) coordination complex.



hemato+ *or (before a vowel)* **hemat+** *comb. form* denoting blood. *Also (esp. Brit.)*: **haemato+**, **haemat+**. *See also* **hemo+**.

hematocrit *or (esp. Brit.)* **haematocrit** **1** *or* **packed red cell volume** the proportion of the volume of a sample of blood that is represented by the red blood cells. **2** an apparatus, essentially a graduated centrifuge tube, used to determine the proportion of the volume of a sample of blood that is represented by the red blood cells.

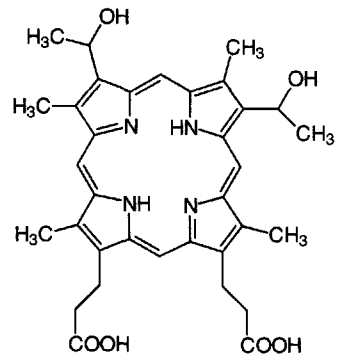
hematocrit technique *or (esp. Brit.)* **haematocrit technique** a method for the rapid isolation of mitochondria or other particles, in which they are separated from the medium by centrifugation through a layer of silicone fluid. The latter is immiscible with water, and of a density intermediate between that of the particles to be separated and that of the medium. A high-density aqueous 'fixative' beneath the silicone layer can be used to stabilize labile compounds in the mitochondria or other particles. *Compare* **hematocrit** (def. 2).

hematology *or (esp. Brit.)* **haematology** the branch of medicine concerned with diseases of the blood or of the blood-forming tissues.

hematolysis *or (esp. Brit.)* **haematolysis** *an alternative name for* **hemolysis**.

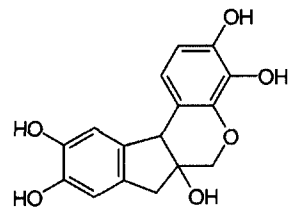
hematopoiesis *or (esp. Brit.)* **haematopoiesis** *an alternative name for* **hemopoiesis**.

hematoporphyrin *or (esp. Brit.)* **haematoporphyrin** *or (formerly)* **hematoporphyrin IX** *or (esp. Brit.)* **haematoporphyrin IX** *the trivial name for* 2,7,12,18-tetramethyl-3,8-bis(1-hydroxyethyl)porphyrin-13,17-dipropionic acid; the porphyrin formed from **heme** (def. 1) or a heme-containing protein on treatment with hydrogen bromide in glacial acetic acid.



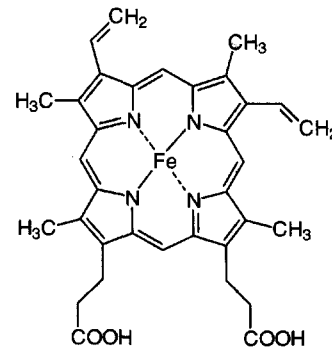
hematoside *or (esp. Brit.)* **haematoside** a **ganglioside**, NeuAc(α2-3)Gal(β1-4)Glc(β1-1)Cer, found in red blood cells.

hematoxylin *or (esp. Brit.)* **haematoxylin** 7,11b-dihydrobenz[*b*]indeno[1,2-*d*]pyran-3,4,6*a*,9,10(6*H*)-pentol; a dye isolated from the heartwood of logwood, *Haematoxylon campechianum* L. Colourless or yellowish, it turns red on exposure to light, and is used as a stain in microscopy.



hematuria *or (esp. Brit.)* **haematuria** the presence of red blood cells in the urine. It can be due to lesions in the urinary tract, but also to glomerular disease of the kidney.

heme *or (esp. Brit.)* **haem** **1** *or* **ferroheme** *or* **ferrohaem** *or* **protoheme** *the trivial name for* **ferroprotoporphyrin** (*formerly called* ferroprotoporphyrin IX); 2,7,12,18-tetramethyl-3,8-divinylporphyrin-13,17-dipropionic acid iron(II) coordination complex. It occurs free and as the prosthetic group of a number of hemoproteins, e.g. hemoglobins, erythrocruorins, myoglobins, some peroxidases, catalases, and cytochromes *b*. *Compare*



heme (def. 1)

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hematin (def. 1), **hemin** (def. 1). **2** *the generic name for* any iron–porphyrin coordination complex irrespective of the valence state of the iron atom (which may be specified). The name of an individual heme is derived from that of the corresponding porphyrin; e.g. cytoheme (from cytoporphyrin) and ferroprotoheme (from protoporphyrin). For biosynthesis, *see* **tetrapyrrole**.

heme–heme interaction *or (esp. Brit.)* **haem–haem interaction** the cooperative interaction between the various heme binding sites for dioxygen molecules that occurs when dioxygen binds with hemoglobin; as oxygenation proceeds, the combination of additional dioxygen molecules is made easier.

heme pocket *or (esp. Brit.)* **haem pocket** a hydrophobic crevice in the tertiary structure of myoglobin, or of a subunit of hemoglobin, into which the heme group fits. The nonpolar vinyl side chains of the heme are buried in the interior of the pocket, while the hydrophilic propionate side-chains project out of the pocket towards the surface of the molecule.

heme protein *or (esp. Brit.)* **haem protein** *an alternative name for* **hemoprotein**.

hemerythrin *or (esp. Brit.)* **haemerythrin** an oxygen carrier found in a few groups of invertebrates, e.g. sipunculid worms, certain molluscs, and crustaceans. It is a nonheme iron-containing protein, the subunits of which each contain about 113 amino-acid residues. Each monomer has an active site containing two atoms of Fe(II), 0.34 nm apart, between which a dioxygen molecule is thought to fit. The molecule is a homo-octamer. Example from *Themiste dyscritum*: database code HEMT_THEDY, 113 amino acids (13.30 kDa); 3-D structure known.

heme synthetase *see* **ferrochelatase**.

heme–thiolate protein *or (esp. Brit.)* **haem–thiolate protein** *see* **P450**.

hemi+ *prefix* denoting half, or affecting one half. *Compare* **semi+**.

hemiacetal *see* **acetal**.

hemicellulose any or all of the cell-wall polysaccharides that are extractable from wood or other plant material with aqueous alkali (in which cellulose itself is insoluble). Hemicelluloses are chiefly xylans, but other homoglycans or heteroglycans containing hexose and/or pentose residues, uronic acid-containing xylans, and other **pectic substances** may also be present.

hemicystine *an alternative name for* **half-cystine**.

hemicystyl *an alternative name for* **half-cystyl**.

hemidesmosome a specialized cell junction between an epithelial cell and its underlying basal lamina. These resemble **desmosomes** morphologically but are chemically and functionally distinct. Between the cell membrane and the underlying connective tissue is a specialized mat of extracellular matrix sometimes known as the linker. The transmembrane linker proteins belong to the **integrin** family of extracellular matrix receptors rather than the **cadherin** family of cell–cell adhesion proteins found in desmosomes.

hemidiaphragm a muscle preparation widely used for metabolic studies *in vitro*, consisting of either of the two excised and separated left and right halves of the diaphragm, usually from a rat.

hemiketal *see* **acetal**.

Hemimetabola *or* **Exopterygota** one of the two divisions of the subclass Pterygota, comprising those insects, e.g. cockroaches, locusts, and grasshoppers, in which the juvenile forms resemble the adults, except for their lack of fully developed wings. Such insects undergo incomplete metamorphosis. *Compare* **Holometabola**.

hemin *or (esp. Brit.)* **haemin** **1** *or* **ferriheme chloride** *or* **protohemin** *the trivial name for* ferriprotoporphyrin chloride (*formerly called* ferriprotoporphyrin IX chloride); chloro(protoporphyrinato)iron(III); chloroiron(III) protoporphyrinate. *Compare* **heme** (def. 1), **hematin** (def. 1). **2** *the generic name for* any chloro(porphyrinato)iron(III) coordination complex.

hemiport a model of translocation of solutes across membranes, based on the possibility that there is interaction through the membrane between superficially disposed protein subunits. These subunits are envisaged as being embedded within the bimolecular lipid layer, anchored to the aqueous phase, and perhaps mobile in the plane of each face of the membrane. The subunits bind the solute in question and, when associated with the symmetrical protein at the opposite face of the membrane, transfer the solute across the membrane.

hemithioacetal *see* **acetal**.

hemithioketal *see* **acetal**.

hemizygous describing an organism in which a gene is present only once in a genotype, as a gene in a haploid cell or organism, a sex-linked gene in the heterogametic sex, or a gene in a segment of chromosome in a diploid cell or organism where its partner segment has been deleted. —**hemizygosity** *n.*

hemo+ *or* **hema+** *or (before a vowel)* **hem+** *comb. form* denoting blood. *Also (esp. Brit.)*: **haemo+**, **haema+**, **haem+**. *See also* **hemato+**.

hemochromatosis *or (esp. Brit.)* **haemochromatosis** a disease of humans characterized by an abnormal, widespread, massive accumulation of tissue iron associated with characteristic pathological changes of tissue structure and function. **Primary hemochromotosis** is a specific genetically determined disease in which hemochromatosis occurs as a result of increased absorption of iron from a normal diet. **Secondary hemochromatosis** results from an increased intake and accumulation of iron secondary to other causes. *Compare* **hemosiderosis**.

hemochrome *or (esp. Brit.)* **haemochrome** any iron–porphyrin coordination complex with one or more strong-field axial ligands (e.g. pyridine).

hemochromogen *or (esp. Brit.)* **haemochromogen** any compound of heme with a nitrogenous base such as a protein (whether native or denatured) or pyridine, typically with two absorption bands in the green part of the visible spectrum. *See also* **chromogen**.

hemocuprein *or (esp. Brit.)* **haemocuprein** *an alternative name for* **superoxide dismutase**.

hemocyanin *or (esp. Brit.)* **haemocyanin** a blue, copper-containing oxygen carrier present in many molluscs and arthropods. It is a nonheme protein that binds one dioxygen molecule for two Cu(I) atoms; the dioxygen molecule is thought to form a bridge between the two copper atoms. The oxygenated compound is very bright blue with an intensity of light absorption 5–10 times that of other known copper complexes. Example from the lobster *Panulirus interruptus*: hexamer of a number of different chains, of which A, B (88% identity between these two), and C have been identified: chain A, database code HCYA_PANIN, 657 amino acids (75.61 kDa); this contains two copper-binding sites (His ligands); two CuA motifs; two other motifs form an oxygen-binding domain; one CuB motif.

hemocyte *or (esp. Brit.)* **haemocyte** any blood cell, especially of an invertebrate animal.

hemocytometer *or (esp. Brit.)* **haemocytometer** an apparatus for counting the number of cells in a known volume of blood. It consists of a slide with a chamber of known depth; the base of the chamber is ruled with a graticule over which the cells can be enumerated under a microscope.

hemodialysis *or (esp. Brit.)* **haemodialysis** the process of separating low-molecular-mass solutes from blood by **dialysis** through a semipermeable membrane, as in an artificial kidney machine.

hemoglobin *or (esp. Brit.)* **haemoglobin** *symbol*: Hb; any of a group of red, iron-containing, oxygen-carrying pigments of the blood of vertebrates and some invertebrates; hemoglobin also occurs in the root nodules of leguminous plants. All vertebrate hemoglobins consist of two pairs of associated **globin** polypeptide chains, each polypeptide chain carrying a heme prosthetic group bound noncovalently, the iron atom of which is in the ferrous state and forms a coordination complex with the pyrrole nitrogens. All normal human hemoglobins contain one pair of 15.7 kDa α chains, of 141 amino-acid residues, and

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a pair of varying 16.5 kDa polypeptide chains, of 146 amino-acid residues and of similar amino-acid sequences. In adult human blood, 98% of the total hemoglobin is Hb A (or Hb A_1), containing a pair of β chains, i.e. it has the composition $\alpha_2\beta_2$, and 2% is Hb A_2, containing a pair of δ chains, i.e. $\alpha_2\delta_2$. In fetal blood, from about 10 weeks to 30 weeks of gestation, >90% of the hemoglobin is Hb F, containing a pair of γ chains, i.e. $\alpha_2\gamma_2$. In embryonic blood, the second pair of chains are ε chains, i.e. the structure is $\alpha_2\varepsilon_2$. Each of the four heme groups in a hemoglobin molecule is able to combine reversibly with one dioxygen molecule; the oxygen-saturation curve of hemoglobin is sigmoidal, showing that there is positive cooperativity between the subunits. The hemoglobin molecule has a two-fold axis of symmetry, each half containing one α chain and one non-α chain; the overall shape of the molecule is globular with the heme groups buried in pockets in the polypeptide chains. There are eight helical regions, called A to G. The histidine at position F8 (i.e. the eighth residue in helix F) is the fifth ligand of the heme Fe(II). Upon oxygenation, dioxygen becomes the sixth ligand of Fe(II) and is also hydrogen bonded to HisE7 with an accompanying conformational change. In the absence of the correct bonding with the globin side chains, Fe(II) autooxidizes to Fe(III) and can no longer bind dioxygen. Examples: human and chimpanzee α chain, database code HBA_HUMAN, 141 amino acids (15.11 kDa); among α chain variants are Luxembourg, Ann Arbor, and Hirosaki; β chain, database code HBB_HUMAN, 146 amino acids (15.85 kDa). Among the **hemoglobinopathies** associated with β-chain variants is **sickle-cell anemia**. In those invertebrates that have hemoglobin (not **hemocyanin**) there is a polymeric hemoglobin. Example from earthworm, 12 subunits arranged in a hexagonal bilayer structure of 3.8 MDa; each one-twelfth subunit is composed primarily of disulfide-linked trimers (chains A, B, and C) and monomers (chain D); D chain, database code GLB1_LUTME, 142 amino acids (16.11 kDa). *See also* **hemoglobin A_{1c}**.

hemoglobin A_{1c} *or (esp. Brit.)* **haemoglobin A_{1c}** *abbr.*: Hb A_{1c}; the most abundant of the **glycated hemoglobins**, which are present in normal adult hemoglobin as minor components (together they represent 3–5% of the total hemoglobin of the erythrocyte). Hb A_{1c} is formed from Hb A_1 subsequent to biosynthesis by glycosylation of one of the two β chains, by a nonenzymic mechanism involving formation of an N-substituted aldimine (Schiff's base) between the amino group of the peptide chain and the aldehyde group of glucose, followed by an **Amadori rearrangement** to the corresponding N-substituted ketoimine (aminodeoxyfructose derivative) (*see also* **Maillard reaction**). In inadequately controlled **diabetes mellitus** the steady-state concentration of Hb A_{1c} in serum is 2–3 times higher than normal, possibly reflecting an abnormally high mean blood glucose concentration during the preceding few months. Other glycosylated hemoglobins change very little in concentration in diabetes; thus measurement of serum levels of Hb A_{1c} is considered to be useful in assessing the degree of control of the condition.

hemoglobinopathy *or (esp. Brit.)* **haemoglobinopathy** any of many types of genetic disorder involving globin, the protein moiety of **hemoglobin**. These are divided into **thalassemia** syndromes, caused by defective synthesis of the component polypeptides of globin, and conditions that arise from mutations leading to amino-acid substitutions in the polypeptide chains. Of the latter there are over 400 known variants, including the classically important **sickle cell** hemoglobin. Many changes lead to increased oxygen affinity, e.g. Hb Rainier (β-145, Tyr → Cys), while in a few instances decreased oxygen affinity occurs, e.g. Hb Kansas (β-102, Asn → Thr). In some cases the substitution leads to an unstable hemoglobin molecule, as in Hb Hammersmith (β-42, Phe → Ser) where the important heme contact of the phenylalanine is lost, leading to the formation of **ferrihemoglobin**, or in Hb Bristol (β-67, Val → Asp) where replacement of the nonpolar valine by aspartic acid causes distortion of the E helix.

hemolin *or (esp. Brit.)* **haemolin** an insect hemolymph protein that is of the immunoglobulin superfamily. It is induced by bacteria. It contains four internal immunoglobulin-type repeats. Example (precursor) from the moth *Hyalophora cecropia*: 413 amino acids (45.78 kDa).

hemolymph *or (esp. Brit.)* **haemolymph** a fluid occurring in the secondary body cavity (coelom) of some invertebrates, considered as functionally equivalent to the blood and lymph of higher animals.

hemolysate *or (esp. Brit.)* **haemolysate** a preparation obtained by lysis of erythrocytes.

hemolysin *or (esp. Brit.)* **haemolysin** **1** any substance, e.g. an antibody, that causes hemolysis. **2** any bacterial exotoxin that ruptures blood-cell membranes. Examples are the products of chromosomal genes of certain hemolytic *Escherichia coli* strains that cause predominantly nongastrointestinal (e.g. urinary tract) infections. There are four genes: *hlyA* encodes hemolysin (Ca^{2+}-binding toxin): database code HLY1_ECOLI, 1023 amino acids (109.75 kDa); *hlyB* encodes an **ABC transporter** for HlyA export: database code HLY2_ECOLI, 707 amino acids (79.77 kDa); *hlyC* encodes a protein involved in hemolysin export: database code HLY3_ECOLI, 170 amino acids (19.70 kDa); *hlyD* encodes a transmembrane protein component of the HlyA export system: database code HLY4_ECOLI, 478 amino acids (54.53 kDa).

hemolysis *or (esp. Brit.)* **haemolysis** the lysis of red blood cells, either *in vivo* or *in vitro*. —**hemolyse** *or* **haemolyse** *vb.*

hemolytic *or (esp. Brit.)* **haemolytic** **1** of, or pertaining to **hemolysis**. **2** an agent or condition that causes hemolysis.

hemopexin *or (esp. Brit.)* **haemopexin** a 57 kDa β_1-glycoprotein of human blood serum with one high-affinity binding site for **heme** (def. 1). The heme complex can be reduced with dithionite to give a three-band absorption spectrum characteristic of ferrohemochrome. Hemopexin may be necessary for heme to be taken up and degraded in the liver.

hemophilia *or (esp. Brit.)* **haemophilia** any of various hereditary disorders in which there is a deficiency or defect in certain of the **blood coagulation** factors resulting in prolonged bleeding following injury. Classical hemophilia, or **hemophilia A**, is a condition in which the blood has a prolonged clotting time due to an abnormally slow conversion of prothrombin to thrombin. It is caused by a functional deficiency of antihemophilic factor (factor VIII), inherited as an X-linked recessive trait. Other deficiencies in the blood coagulation system, e.g. **Christmas disease**, or **hemophilia B**, due to a deficiency of factor IX, produce similar clinical pictures.

hemopoiesis *or* **hematopoiesis** the process of blood formation, especially the formation of blood cells, occurring mainly in bone marrow. *Also (esp. Brit.)*: **haemopoiesis**, **haematopoiesis**. —**hemopoietic**, **hematopoietic** *or* **haemopoietic**, **haematopoietic** *adj.*

hemoprotein *or* **heme protein** any protein to which an iron–porphyrin compound is linked in a stoichiometric manner. Hemoproteins include hemoglobins, myoglobins, cytochromes, catalase, and some peroxidases. *Also (esp. Brit.)*: **haemoprotein**, **haem protein**.

hemorphin *or (esp. Brit.)* **haemorphin** any of a group of hemoglobin-derived peptides with affinity for opioid receptors.

hemorrhage *or (esp. Brit.)* **haemorrhage** bleeding; the escape of blood from a ruptured blood vessel, either externally or internally. —**hemorrhagic** *or (esp. Brit.)* **haemorrhagic** *adj.*

hemorrhagic toxin C and D *see* **atrolysin C**.

hemosiderin *or (esp. Brit.)* **haemosiderin** an insoluble, granular, ill-defined complex formed by the denaturation of **ferritin** with associated loss of apoferritin and micellar aggregation; about one third of its mass is iron. Hemosiderin occurs in liver, spleen, and red bone marrow, its amount increasing with increased iron content of the body. It is responsible for the histochemical staining of tissue by the Prussian Blue reaction, a deep-blue ferric ferrocyanide ($Fe^{III}[Fe^{II}(CN)_6]$). The distribution of stored iron is shifted from ferritin to hemosiderin in

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direct correlation with ascorbic acid deficiency. *See* **iron overload**.

hemosiderosis *or (esp. Brit.)* **haemosiderosis** an abnormal increase in tissue iron content due to some defect in the control of iron turnover in the body or to increased iron ingestion. It is not associated with pathological changes in tissue structure and function. *Compare* **hemochromatosis**.

hemostasis *or (esp. Brit.)* **haemostasis** **1** the stopping of bleeding or the arrest of the circulation to an organ or part. **2** the stagnation of blood in an organ or part.

hemostat *or (esp. Brit.)* **haemostat** a device or a chemical agent that stops or retards bleeding.

hemostatic *or (esp. Brit.)* **haemostatic** **1** of, relating to, or functioning to cause **hemostasis** (def. 1). **2** a drug or other agent that retards or stops bleeding.

Hench, Philip Showalter (1896–1965), US physician notable for his demonstration (with E. C. Kendall) that rheumatoid arthritis could be treated with an adrenal hormone (later known as cortisone); Nobel Laureate in Physiology or Medicine (1950) jointly with E. C. Kendall and T. Reichstein 'for their discoveries relating to the hormones of the adrenal cortex, their structure and biological effects'.

Henderson–Hasselbalch equation an equation relating pH to the composition of buffer solutions:

$$pH = pK_A + \log([\text{conjugate base}]/[\text{acid}]),$$

where pK_A is the common logarithm of the acid dissociation constant of the buffer acid. The following approximation is often used:

$$pH = pK_A + \log([\text{salt}]/[\text{acid}]).$$

[After Lawrence Joseph Henderson (1878–1942), US physician and biochemist, and Karl A. Hasselbalch (1874–), Danish biochemist, who together formulated the equation in 1910.]

henna a preparation obtained from the dried and powdered leaves of *Lawsonia alba*, *L. inermis*, or *L. spinosa*, widely used for dyeing hair and fingernails. The active ingredient is **lawsone**.

henry (*pl.* **henrys** *or* **henries**) *symbol*: H; the SI derived unit of inductance, equal to the inductance of a closed circuit with a **magnetic flux** of 1 weber per ampere of current,

$$H = Wb\ A^{-1}\ s = m^2\ kg\ s^{-2}\ A^{-2}$$

[After Joseph Henry (1797–1878), US physicist.]

Henry's function a function used in the theoretical treatment of the electrophoretic mobility of macromolecules that is dependent on the radius of the macromolecule, r, and its reciprocal ion-atmosphere radius, κ (derived from **Debye–Hückel theory**). It varies between 1.0 and 1.5 as κr goes from zero to infinity.

Henry's law the principle that the concentration of a gas in solution, at constant temperature, is directly proportional to the partial pressure of the gas in the vapour phase in equilibrium with that solution. It holds with high precision for gases of low solubility at pressures below approximately 10^5 Pa. It may be expressed by: $c_G = kp_G$, where c_G is the molar concentration of the gas in solution, p_G is the partial pressure of the gas in the gas phase, and k is a proportionality constant. [After William Henry (1774–1836), British chemist.]

heparan any polysaccharide derived by desulfation of **heparan sulfate** or **heparin**.

heparan sulfate any member of a group of glycosaminoglycans that have repeat units consisting of alternating α1→4-linked hexuronic acid and glucosamine residues, the former being a mixture of sulfated and nonsulfated D-glucuronic and L-iduronic acids, and the latter being either sulfated or acetylated on its amino group as well as sulfated on one of its hydroxyl groups. They usually occur attached to protein to form proteoglycans, the mode of attachment being through a xylose residue as in **chondroitin sulfates**. Heparan sulfate accumulates in a number of the mucopolysaccharidoses, e.g. Hunter syndrome, Hurler syndrome, and Sanfilippo syndrome. *See* **mucopolysaccharidosis**. *See also* **heparin**.

heparan sulfate proteoglycan core protein *abbr.*: HSPG core protein; any of a group of modular heparan sulfate proteoglycan proteins with three heparan sulfate chains. Also known as **perlecans**, they have domains with homology to the low-density lipoprotein receptor, epidermal growth factor, laminin, and neural cell adhesion molecule, and have 15 immunoglobulin-like domains. Examples from *Mus musculus*: database code S18252, 3707 amino acids (397.85 kDa), and database code PGBM_MOUSE, 2481 amino acids (270.81 kDa).

heparin any member of a group of glycosaminoglycans found mainly as an intracellular component of mast cells. They are similar to **heparan sulfates** but are of somewhat higher average M_r (6000–20 000) and contain fewer *N*-acetyl groups and more *N*-sulfate and *O*-sulfate groups; they may be attached in the same manner to protein, forming proteoglycans. They consist predominantly of alternating α1→4-linked D-galactose and *N*-acetyl-*D*-glucosamine-6-sulfate residues. Heparins are secreted into the bloodstream by the mast cells of liver, lung, and other tissues; they act as inhibitors of blood clotting by activating **antithrombin III**.

heparinize *or* **heparinise** to treat with a preparation of **heparin**, usually as its sodium or lithium salt, in order to prevent clotting, either *in vivo* or *in vitro*, of blood or blood plasma. —**heparinization** *or* **heparinisation** *n.*

hepat+ *a variant form of* **hepato+** (before a vowel).

hepatectomy surgical removal of the liver. In **partial hepatectomy**, only some of the lobes of the liver are removed; this causes the remaining lobes to regenerate so that the liver *in toto* regains its former weight. —**hepatectomize** *or* **heparectomise** *vb.*

hepatic of, or pertaining to, the liver.

hepatitis any inflammatory disease of the liver. In humans the most common cause is infection with a virus or an amoeba. The three most common forms of viral infectious hepatitis are designated A, B, and C. Hepatitis A is caused by a single-stranded RNA **picornavirus**, for which there is now a killed virus vaccine, the virus having been grown in tissue culture. Hepatitis B is caused by a double-stranded DNA virus of the Hepadnaviridae family. The causative agent is a spherical virion with a diameter of 42 nm, often referred to as the **Dane particle**. This virus is especially virulent and its presence is associated with the development of primary liver tumours – the incidence of these is particularly high in China. The antigens may be in the form of 22 nm diameter, spherical particles designated HBsAg; principal components include gp27, which is a glycosylated form of p24, and a 42 kDa protein, database code VMSA_HPBVA, 389 amino acids (42.73 kDa). HBsAg is produced in recombinant yeast, the 22 nm particles being similar to those found in the plasma of infected individuals. These provide a very effective vaccine. Hepatitis C, formerly called 'non-A non-B', is caused by a single-stranded RNA virus, for which there is as yet no vaccine. Another form, hepatitis D, can be controlled by the vaccine to hepatitis B, and there are probably three other types: E, F, and G, of which G has recently been characterized.

hepato+ *or (before a vowel)* **hepat+** *comb. form* denoting of or pertaining to the liver.

hepatocarcinogen any **carcinogen** that acts specifically or primarily on liver.

hepatocellular of, or pertaining to **hepatocytes**.

hepatocyte *or (formerly)* **parenchymal liver cell**. the major (but not the only) cell type of the liver. They are arranged in folded sheets facing blood-filled spaces called sinusoids. Hepatocytes are responsible for the synthesis, degradation, and storage of a wide range of substances. They are the site of synthesis of all the plasma proteins, except for antibody, and are the site of storage of **glycogen**.

hepatocyte growth factor *abbr.*: HGF; *other name*: scatter factor; a **cytokine** produced by platelets, fibroblasts, macrophages, endothelial cells, and smooth muscle cells that is a po-

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tent **mitogen** for hepatocytes, epithelial cells, keratinocytes, melanocytes, and hematopoietic precursor cells. It is a glycoprotein, with four **kringle** domains and no known protease activity. The molecule is a disulfide-linked dimer of α (463 amino acids) and β (234 amino acids) subunits, which are derived from a common precursor. Example from human: database code HGF_HUMAN, 728 amino acids (83.04 kDa).

hepatocyte growth factor receptor a type I membrane protein that binds **hepatocyte growth factor** and mediates its intracellular action by a protein tyrosine kinase (EC 2.7.1.112) activity on its intracellular domain. It is encoded by the *MET* protooncogene, and comprises a dimer of two subunits, α and β. Example (precursor) from human: database code KMET_HUMAN, 1390 amino acids (155.35 kDa). *See also* ***tpr-met***.

hepatoflavin *or* **hepatoflavine** *a former name for* **riboflavin**.

hepatolenticular degeneration *an alternative name for* **Wilson's disease**.

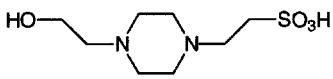
hepatoma any **carcinoma** derived from liver cells.

hepatopancreas a digestive gland, found in many invertebrates, that performs functions similar to those of the liver and the pancreas in vertebrates.

hepatosis any noninflammatory disease of the liver.

hepatotoxin any toxin that acts specifically or primarily on the liver.

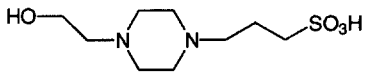
Hepes *or* **HEPES** *abbr. for (and trivial name of)* 4-(2-hydroxyethyl)-1-piperazine-ethanesulfonic acid; a **Good buffer substance**, pK_a (20 °C) = 7.55.



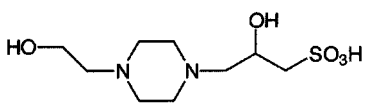
hepoxilin *abbr.*: Hx; any of various epoxyhydroxy metabolites of 12-hydroperoxyeicosatetraenoate, e.g. 13-hydroxy-14,15-epoxyeicosatetraenoate. A number of sites of formation have been reported, activities including modulation of neurotransmission in brain and release of insulin in pancreatic islets.

hepoxilin-epoxide hydrolase EC 3.3.2.7; an enzyme that converts (5*Z*,9*E*,14*Z*)-(8ξ,11*R*,12*S*)-11,12-epoxy-8-hydroxyeicosa-5,9,14-trienoate **hepoxilin** A_3 to the trioxilin, (5*Z*,9*E*,14*Z*)-(8ξ,11ξ,12*S*)-8,11,12-trihydroxyeicosa-5,9,14-trienoate (trioxilin A_3).

Hepps *or* **HEPPS** *or* **EPPS** *abbr. for (and trivial name of)* 4-(2-hydroxyethyl)-1-piperazinepropanesulfonic acid; a **Good buffer substance**, pK_a (20 °C) = 8.0.



Heppso *or* **HEPPSO** *abbr. for (and trivial name of)* 4-(2-hydroxyethyl)-1-piperazine-(2-hydroxypropanesulfonic acid); a **Good buffer substance**, pK_a (25 °C) = 7.8.



hepsin EC 3.4.21.–; a serine protease, similar to other trypsin-like enzymes, that is a type II membrane protein. It is required for growth and maintenance of cell morphology in many tissues. Example from human: database code HEPS_HUMAN, 417 amino acids (44.96 kDa).

hepta+ *or (before a vowel)* **hept+** *comb. form* denoting seven.

heptanoate **1** the anion, CH_3–$[CH_2]_5$–COO^-, derived from heptanoic acid (formerly enanthic acid). **2** any salt or ester of heptanoic acid.

heptanoyl *symbol*: Hpo; the univalent acyl group, CH_3–$[CH_2]_5$–CO–, derived from heptanoic acid.

heptitol any **alditol** having a chain of seven carbon atoms in the molecule.

heptose any **aldose** having a chain of seven carbon atoms in the molecule.

heptulose any **ketose** having a chain of seven carbon atoms in the molecule.

heptyl *symbol*: Hp; the alkyl group, CH_3–$[CH_2]_5$–CH_2–, derived from heptane.

heptyl glucoside *n*-heptyl β-D-glucopyranoside; a nonionic detergent, CMC 79 mM.

heptyl thioglucoside *n*-heptyl 1-thio-β-D-glucopyranoside; a nonionic detergent; the CMC, 30 mM, remains unchanged between 1 and 20 °C.

HER2 *see* ***neu***.

herbicide any chemical substance that destroys plants or inhibits their growth, especially one used to control weeds.

hereditary of, pertaining to, or caused by **heredity**; inherited.

hereditary disease any pathological condition that is caused by the presence in the organism of an abnormal gene.

hereditary fructose-bisphosphatase deficiency an inherited autosomal recessive condition in humans characterized by less than 20% of normal activity of **fructose-bisphosphatase** (EC 3.1.3.11). It is characterized in infants by episodic spells of hyperventilation, apnoea, hypoglycemia, ketosis, and lactic acidosis. Surviving infants appear to become normal, but gluconeogenesis in their livers is severely impaired, and when glycogen stores are depleted, amino acids, lactate, and ketones accumulate. Subjects are not sensitive to fructose intake. *Compare* **hereditary fructose intolerance**.

hereditary fructose intolerance a condition in humans, inherited as an autosomal recessive character, in which there is a deficiency of the aldolase-B isoenzyme of **fructose-bisphosphate aldolase** (EC 4.1.2.13) (there is less than 15% normal activity with fructose 1-phosphate as substrate but activity is less depressed with fructose 1,6-bisphosphate as substrate) while the levels of aldolases A and C are normal (*see* **aldolase** (def. 2)). The condition is characterized by severe hypoglycemia and vomiting shortly after fructose intake. In this condition prolonged fructose ingestion in infants leads to poor feeding, vomiting, hepatomegaly, jaundice, hemorrhage, proximal-renal-tubule syndrome, and death. The hypoglycemia ensuing after fructose ingestion is caused by fructose 1-phosphate inhibition of glycogenolysis at the phosphorylase level and of gluconeogenesis at the mutant aldolase level. *Compare* **hereditary fructose-bisphophatase deficiency**.

heredity **1** the transmission from one generation to another of genetic factors that determine the characteristics of an organism. **2** all of the inherited factors in an organism or all the characteristics determined by them.

heregulin *abbr.*: HRG; one of several glycoproteins that bind to the transmembrane tyrosine kinase ErbB2 p185 and stimulate its activity. They are secreted by human breast cancer cells in culture. Example heregulin-α precursor from human: database code A43273, 640 amino acids (70.29 kDa).

hermone *an alternative term for* **hormone** (suggested by E. Schäfer in 1913 as better expressing the concept of chemical messengers).

heroin *see* **diacetylmorphine, morphine**.

herpes virus any of a family (Herpesviridae) of enveloped, icosahedral, double-stranded DNA viruses, many of which infect animals. The family includes human herpesviruses types 1 and 2, Epstein–Barr virus, zoster (varicella) virus, pseudorabies virus, cytomegalovirus, Lucke virus, and Marek's disease virus.

herring any marine fish of the family Clupeidae, the flesh of

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which is comparatively rich in oils with a high content of long-chain *n*-3 **fatty acids**; typical composition (range of major fatty acids, expressed as % of total fatty acids): 16:0, 12–18%; 16:1(*n*-7), 6–8%; 18:1(*n*-9), 11–25%; 20:1(*n*-9), 7–19%; 20:5(*n*-3), 11–15%; 22:6(*n*-3), 5–8%.

Hershey, Alfred Day (1908–97), US geneticist; Nobel Laureate in Physiology or Medicine (1969) jointly with M. Delbrück and S. E. Luria 'for their discoveries concerning the replication mechanism and the genetic structure of viruses'.

Hershey–Chase experiment a seminal experiment, reported in 1952, in which it was demonstrated that when an *Escherichia coli* cell is infected with T2 bacteriophage, the phage DNA is injected into the cell whereas the phage coat protein remains on the outside of the infected bacterial cell. This was shown by demonstrating that most of the ^{35}S-labelled phage protein could be removed from the surface of the bacterial cells by application of a shearing force without removing the ^{32}P-labelled nucleic acid and without interfering with the course of productive infection. The phage nucleic acid could be shown to have moved into the bacterial cell. It was therefore concluded that only the phage DNA was required for infection, indicating that DNA must be the hereditary material. This confirmed earlier experiments in 1944 by Avery and colleagues (*see* **transforming principle**), but was somewhat more readily accepted when Watson and Crick deduced the structure of DNA. [After A. D. Hershey and Martha Chase (1927–).]

Hershey circle a circular duplex DNA structure in which each strand contains one interruption and in which the interruptions are not opposite each other. It is formed by some linear, double-stranded DNA molecules (e.g. from *Escherichia coli* phage λ) containing short, complementary single strands (cohesive ends) at each end when these cohesive ends base-pair with each other.

Hers's disease *an alternative name for* type VI **glycogen disease**.

hertz *symbol*: Hz; the SI derived unit of **frequency** of a periodic phenomenon, equal to 1 cycle per second; i.e. 1 Hz = 1 s^{-1}. [After Heinrich Hertz (1857–94), German physicist.]

Hertz, Gustav (1887–1975), German physicist; Nobel Laureate in Physics (1926) jointly with J. Franck 'for their discovery of the laws governing the impact of an electron upon an atom'.

Hess's law of constant heat summation the statement that the enthalpy change in a chemical reaction is the same whether the reaction takes place in one stage or in more than one stage. [After Germain Henri Hess (1802–50), Genevese-born Russian chemist; known in Russia as German Ivanovich Gess.]

HETE *abbr. for* hydroxyeicosatetraenoate; *see also* **dihydroxyeicosatetraenoate**.

hetero+ *comb. form* **1** other, different, unusual. *Compare* **allo+** (def. 1), **homo+** (def. 1), **iso+** (def. 1), **xeno+** (def. 1). **2** for, from, or directed towards a different species. *Compare* **allo+** (def. 2), **homo+** (def. 2), **iso+** (def. 2), **xeno+** (def. 2). **3** containing atoms, groups, linkages, residues, or subunits of different kinds. **4** being or pertaining to an atom other than the predominant or significant one, especially of a nitrogen, oxygen, or sulfur atom in a ring containing mainly carbon atoms. *Compare* **homo+** (def. 4).

heteroantibody any antibody (including any autoantibody) that is able to react with an antigen derived from another species. *Compare* **isoantibody**.

heteroantigen any antigen derived from one species that is able to stimulate an immune response in another species. *Compare* **isoantigen**.

heteroatom any atom in the chain or ring of an organic compound that is not a carbon atom. —**heteroatomic** *adj.*

heterobifunctional describing any reagent that carries two differing reactive groups. *Compare* **homobifunctional**.

heterocaryon *a variant spelling of* **heterokaryon**.

heterochromatic **1** relating to or possessing more than one colour; relating to light or other electromagnetic radiation of more than one frequency. *Compare* **monochromatic**. **2** of, relating to, or possessing **heterochromatin**.

heterochromatin a condensed form of **chromatin**, occurring in the nucleus at interphase, that stains strongly with basophilic dyes. The DNA of heterochromatin is replicated at a later stage in the cell-division cycle than **euchromatin**. 'Satellite' DNA is associated with heterochromatin, and the sex chromosomes of animals, especially the Y chromosome, contain large regions of heterochromatin. *Compare* **euchromatin**.

heteroconjugation the association between a base and the conjugate acid of a different base through a hydrogen bond. *See* **conjugate acid–base pair**. *Compare* **homoconjugation**.

heterocycle any compound or molecular structure that is **heterocyclic** (def. 1); a **heterocyclic** (def. 2).

heterocyclic **1** describing any cyclic molecular structure containing atoms of at least two different elements in the ring or rings; describing any compound having such a structure. *Compare* **carbocyclic** (def. 1), **homocyclic** (def. 1). **2** *or* **heterocycle** any such compound.

heterocyst any of the clear cells that occur at intervals on the filaments of certain cyanobacteria. They are thought to be important sites of nitrogen fixation.

heterodetic describing a cyclic peptide in which the ring consists of amino-acid residues only, but the linkages forming the ring are not solely eupeptide bonds; one (or, if nonproximate, more than one) is an isopeptide, disulfide, ester, or other bond. *Compare* **homodetic**.

heterodimer any molecular structure in which two nonidentical subunits are associated. *Compare* **dimer**, **homodimer**.

heteroduplex **1** any double-stranded DNA in which the two strands do not have completely complementary base sequences. In a **mutational heteroduplex** a mutational event has occurred in one of the polynucleotide chains; such a molecule does not produce uniform progeny on replication. A **recombinational heteroduplex** is a double-stranded DNA molecule that gives rise to one parental and one recombinant molecule of DNA in the reproductive cycle that immediately follows its production. Heteroduplex DNA may also arise from annealing DNA single strands *in vitro*. **2** a DNA–RNA hybrid. *Compare* **homoduplex**.

heteroduplex mapping the physical mapping of the base sequence homology of two DNA molecules. It is accomplished after the *in vitro* formation of a hybrid double-stranded molecule, in which one polynucleotide strand is from one of the DNA molecules and the complementary polynucleotide strand is from the other. Unpaired single-stranded regions are located and measured by electron microscopy.

heterogametic describing the sex whose cell nuclei contain a pair of dissimilar **sex chromosomes**. The heterogametic sex is usually male in mammals but is female in the Lepidoptera, birds, reptiles, some amphibians and fishes, and a few plants. *Compare* **homogametic**.

heterogeneous **1** differing in kind, as in a heterogeneous population. **2** describing a group of molecules that is not uniform with respect to size, charge, structure, or other property. **3** describing a system consisting of two or more phases. *Compare* **heterogenous**. —**heterogeneity** *n.*

heterogeneous catalysis any catalytic system in which the catalyst constitutes a different phase from that of the reactants. *Compare* **homogeneous catalysis**.

heterogeneous immunoassay any form of **immunoassay** that involves physical separation, at some stage of the procedure, of antibody-bound antigen from remaining free antigen. It includes **radioimmunoassay**. *Compare* **homogeneous immunoassay**.

heterogeneous nuclear ribonucleoprotein *abbr.*: hnRNP; particulate complexes of **heterogeneous nuclear RNA** (hnRNA) with proteins, which are cell-specific and themselves heterogeneous. The protein component may play a role in the processing of the hnRNA to mRNA.

heterogeneous nuclear RNA *abbr.*: hnRNA *or* HnRNA *or* H-RNA; a heterogeneous mixture of RNA molecules of high M_r with a rapid turnover rate that occurs in cell nuclei during protein synthesis. It is the form of RNA synthesized in eu-

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karyotes by RNA polymerase II, i.e. that which is translated into protein. It represents the transcription products of both the exons and the introns of a gene or genes and is processed to form mRNA by the removal of the nontranslated portions (corresponding to the introns in the DNA). So-named because heterogeneity in size was one of the first characteristics used to distinguish it from other forms of nuclear RNA.

heterogenesis the production of offspring having different characteristics in successive generations; e.g. the alternation between generations that produce gametes and those that reproduce through agametes or by parthenogenesis.

heterogenetic describing chromosome pairing during meiosis when the pairing partners are derived from different original ancestors. *Compare* **homogenetic**.

heterogenic **1** describing a population or a gamete containing more than one allele of a particular gene. **2** describing two genetic elements that are not known to have a common ancestry. **3** *an alternative word for* **heterogenous**. *Compare* **homogenic**.

heterogenize *or* **xenogenize** to introduce a foreign, especially a more potent, antigen into a cell surface in order to enhance the response by T lymphocytes to other cell-surface antigens. —**heterogenization** *n.*

heterogenous *or* **heterogenic** not originating within the organism in question; of foreign origin. *Compare* **heterogeneous**.

heteroglycan *or* **heteropolysaccharide** any polysaccharide (i.e. glycan) that contains residues of two or more kinds of monosaccharide (i.e. glycose) molecule. *Compare* **homoglycan**.

heterograft *or* **heterologous graft** *an alternative name for* **xenograft**. *Compare* **homograft**.

heteroimmune describing a pair of bacteriophages in which each is sensitive to its own repressor but not to that of the other.

heterokaryon *or* **heterocaryon** any cell with more than one nucleus, in which the nuclei are not all of the same genetic constitution, or a tissue composed of such cells. *Compare* **homokaryon**. —**heterokaryotic** *or* **heterocaryotic** *adj.*

heterokaryosis *or* **heterocaryosis** the association of genetically different nuclei in a common cytoplasm.

heterolactic fermentation a type of fermentation of glucose in which the products include lactate, acetate and/or ethanol, and carbon dioxide. A key enzyme in the pathway is **phosphoketolase**, which cleaves xylulose 5-phosphate (produced by the pentose phosphate pathway) to D-glyceraldehyde 3-phosphate and acetyl phosphate, the former being then converted to lactate while the latter can form acetate and/or ethanol. Organisms that ferment in this manner include *Leuconostoc* spp. and some species of *Lactobacillus*; some produce D(−)-lactate while others produce DL-lactate. *Compare* **homolactic fermentation**.

heterolipid *a former name for* any complex lipid.

heterologous **1** consisting of different elements or of like elements in different proportions. **2** *or* **heterospecific** derived from another species, e.g. heterologous serum or tissue. *Compare* **homologous**, **isologous**.

heterologous association describing any association between two **protomers** in which the **domain of bonding** is made up of two different **binding sets**. *Compare* **isologous**.

heterologous desensitization *see* **desensitization**.

heterologous graft *or* **heterograft** *an alternative name for* **xenograft**.

heterolysin any antibody or other hemolysin formed in response to the introduction of erythrocytes from another species into the bloodstream of an animal. *Compare* **autolysin**, **homolysin**.

heterolysis **1** *(in chemistry)* the cleavage of a bond in such a manner that both bonding electrons remain within one of the two fragments between which the bond is broken; e.g. $A–B \rightarrow A^+ + B^-$. *Compare* **homolysis**. **2** *(in biochemistry)* the lysis of cells or tissues by the action of exogenous agents, e.g. enzymes, detergents, or lysins. *Compare* **autolysis**. —**heterolytic** *adj.*

heterolysosome any early **secondary lysosome** concerned with the digestion of exogenous material (i.e. **heterophagy**). *See* **heterophagosome**.

heteromorphic *or* **heteromorphous** **1** differing from the normal form, e.g. in size, shape, or function. **2** describing the members of any pair of homologous chromosomes that differ from each other in size or shape. **3** *(especially of insects)* having differing forms at different stages of the life cycle. **4** *an alternative term for* **polymorphic**. *Compare* **isomorphic**. —**heteromorphism** *or* **heteromorphy** *n.*

heterooligomer any **oligomer** made up of two or more kinds of constitutional repeating unit. —**heterooligomeric** *adj.*

heterophagosome any **phagosome** containing material exogenous to the cell. Fusion with a lysosome leads to the formation of a heterolysosome. *Compare* **autophagosome**.

heterophagy the process by which cells digest exogenous material that they have taken up. *Compare* **autophagy**. —**heterophagic** *adj.*

heterophilic binding *(of adhesion molecules)* binding of an adhesion molecule in one cell to a non-identical adhesion molecule in an adjacent cell. *Compare* **homophilic binding**.

heteroplasmy the presence of more than one type of mitochondrial DNA in a cell. A mutant mitochondrial DNA may be present in varying amounts so that phenotypic variation between cells is possible.

heteroploid describing a cell that contains any number of chromosomes except the **haploid** or **diploid** number. The term includes all **aneuploid** or **polyploid** numbers of chromosomes.

heteropolymer any polymer made up of two or more kinds of constitutional repeating unit. Proteins are typical heteropolymers. —**heteropolymeric** *adj.*

heteropolysaccharide *an alternative term for* **heteroglycan**.

heteroside *a former name for* any glycoside containing a noncarbohydrate moiety (aglycon).

heterospecific having specificity for or derived from a different species; **heterologous** (def. 2).

heterotetramer any molecular structure that can be dissociated into four (or two pairs of) nonidentical monomers. —**heterotetrameric** *adj.*

heterotope *any of two or more chemical elements having atoms of different atomic number and occupying different places in the periodic table. The term includes* **isobar** (def. 1). *Compare* **isotope**.

heterotopia *or* **heterotopy** the displacement, or unusual position, of a cell, organ, tissue graft, etc.

heterotopic **1** *(in chemistry)* of, relating to, or being a **heterotope** or heterotopes. *Compare* **isotopic**. **2** *(in biology and medicine) or* **heterotopous** displaced or in an unusual anatomical position.

heterotopic transplant any tissue graft that is transplanted from its normal position to another in the same organism. *Compare* **orthotopic transplant**.

heterotopous *a variant form of* **heterotopic** (def. 2).

heterotopy *a variant form of* **heterotopia**.

heterotrimer any molecular structure that is dissociable into three nonidentical monomers. —**heterotrimeric** *adj.*

heterotroph *or* **heterotrophe** *or* **organotroph** any organism whose nutritional requirements are not satisfied solely by simple inorganic substances and for which a supply of organic carbon is required for the synthesis of cellular constituents. Heterotrophs may be subdivided into **chemoheterotrophs** (or chemoorganotrophs) and **photoheterotrophs** (or photoorganotrophs) according, respectively, to whether they are **chemotrophs** or **phototrophs**. *Compare* **autotroph**. —**heterotrophic** *adj.*; **heterotrophy** *n.*

heterotropic **1** describing an **allosteric** effect in which interaction occurs between nonidentical ligands; the effect may be either cooperative or antagonistic. The term is applied also to such an interaction, to an allosteric enzyme for which different substances act as the substrate and the effector, to the regulation of such an allosteric system, etc. *Compare* **homotropic**. **2** describing a chromosome that does not pair with another at meiosis, especially a sex chromosome in the heterogametic sex.

heterotypic pertaining to, or being the first, reductive division in **meiosis**. *Compare* **homeotypic**.

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heterozygosis **1** the union of genetically different gametes to form a **heterozygote**. **2** *or* **heterozygosity** the state or condition of being a heterozygote. *Compare* **homozygosis**.

heterozygosity *an alternative term for* **heterozygosis** (def. 2).

heterozygote any cell or organism having two different genes (alleles) at one or more corresponding loci on homologous chromosomes. With respect to such loci a heterozygote will produce two different types of gametes. *Compare* **homozygote**.

heterozygous *or* **heterozygotic** of, pertaining to, or being a **heterozygote**; hybrid.

HETP *abbr. for* height equivalent to a theoretical plate.

heuristic describing any method for solving mathematical or other problems for which no **algorithm** (or closed method) exists. It involves narrowing down the field of search for a solution by inductive reasoning from past experience of similar problems. *Compare* **stochastic**.

HEV *abbr. for* high-walled endothelium of the post-capillary venules.

hevein an *N*-acetyl-D-glucosamine and *N*-acetyl-D-neuraminic acid binding lectin; it is present in the latex of the rubber tree, *Hevea brasiliensis* and has 56% homology with wheat germ agglutinin. Example (precursor) from *H. brasiliensis*: database code HEMO_HYACE, 413 amino acids (45.78 kDa).

Hevesy, György (Károly) (1885–1966), *also styled, inter alia, as* **Georg (Karl) von Hevesy** *or* **George (Charles) von Hevesy** *or* **George (Charles) Hevesy** *or* **George (Charles) de Hevesy** Hungarian-born Swedish radiochemist, analytical chemist, and biochemist who (with F. A. Paneth in 1913) was the first to recognize the possibility of using natural radioactive elements as indicators and is remembered for his subsequent pioneering researches employing natural and artificial radioisotopes as indicators or tracers in chemical and biological systems and also for the discovery of hafnium; Nobel Laureate in Chemistry (1943) 'for his work on the use of isotopes as tracers in the study of chemical processes'.

hexa+ *or (before a vowel)* **hex+** *comb. form* denoting six, sixfold, six times.

hexabrachion a six-armed structure, characteristic of the **tenascin** molecule. Regions of the protein radiate outwards like spokes of a wheel. [From L. *brachium* arm.]

hexadecadienoic acid any straight-chain fatty acid having sixteen carbon atoms and two double bonds per molecule. (*all-Z*)-Hexadeca-6,9-dienoic acid is found in small amounts in some animal lipids.

hexadecanoic acid *the systematic name for* palmitic acid; *see* **palmitate**.

hexadecenoic acid any straight-chain fatty acid having sixteen carbon atoms and one double bond per molecule. The most common are the 9*Z*-isomer (palmitoleic acid; *see* **palmitoleate**) and the 11*Z*-isomer, but the 3*E*-, 6*E*-, 6*Z*-, 9*E*-, and 10*Z*-isomers are also variously found in animals or plants; the 9*E*-isomer (i.e. palmitelaidic acid) is a pheromone.

hexaethyleneglycol mono-*n*-decyl ether a nonionic detergent; *see* C_xE_y.

hexaethyleneglycol mono-*n*-dodecyl ether a nonionic detergent; *see* C_xE_y.

hexagonal phase (of phospholipids) a phase in which the polar headgroups are orientated towards the interior of a phospholipid aggregate, with the fatty acyl carbon chains pointing outwards; a form of inverted micelle. It can occur in lipid bilayers, especially at higher temperatures. Certain phospholipids, such as phosphatidylethanolamine, have a greater tendency to adopt this phase than, e.g., phosphatidylcholine. A hexagonal phase with the polar headgroups oriented towards the exterior of the micelle can also exist. *See also* **liquid-crystalline phase**, **phase transition**.

hexamer **1** any oligomer consisting of six monomers. **2** the group of six capsomeres in an icosahedral virus capsid.

hexanoate *or* **caproate** **1** the anion, $CH_3–[CH_2]_4–COO^-$, derived from hexanoic acid. **2** any salt or ester of hexanoic acid.

hexanolamino-PAF 1-*O*-hexadecyl-2-*O*-acetyl-*sn*-glycero-3-phospho-(*N*,*N*,*N*-trimethyl)-hexanolamine; a substance that inhibits the effects induced by **platelet activating factor**, including platelet aggregation, secretion, and inositol phospholipid turnover; superoxide ion and H_2O_2 release from macrophages; hepatic glycogenolysis; and vasoconstriction.

hexanoyl *or (formerly)* **caproyl** *symbol*: Hxo; the univalent acyl group, $CH_3–[CH_2]_4–CO–$, derived from hexanoic acid. *See* **caproyl** (def. 2).

hexaric acid an **aldaric** acid formally derived from a hexose by oxidation at both C-1 and C-6.

hexitol any **alditol** having a chain of six carbon atoms in the molecule.

hexokinase EC 2.7.1.1; *systematic name*: ATP:D-hexose 6-phosphotransferase; *other name* (used for hexokinase IV): glucokinase; the phosphotransferase enzyme that catalyses the phosphorylation by ATP of D-hexose to form D-hexose 6-phosphate and ADP. In vertebrates there are four major isoenzymes, designated hexokinase types I, II, III, and IV, also called hexokinases A–D. All of these types are relatively nonspecific with respect to sugar, and phosphorylate a number of hexoses such as glucose, fructose, and mannose. Thus the name glucokinase for type IV may mislead. Types I–III all have $M_r \approx 100$ kDa and are sensitive to the product, glucose 6-phosphate (*abbr.*: Glc-6-*P*). They differ from hexokinases found in yeast, which have $M_r \approx 50$ kDa, and are not inhibited by Glc-6-*P*. Type III is inhibited by excess glucose. Type IV, despite being a monomer with only one active site, shows cooperativity with respect to glucose, and reaches physiologically significant activity at higher glucose concentrations than types I–III. In hepatocytes, at less than 5 mM glucose it is present as an inactive enzyme bound to a regulatory protein; a glucose concentration of 15 mM causes translocation and activation of the enzyme. Type II is the major isoenzyme of skeletal muscle and adipose tissue. There are strong sequence similarities between the different types. The mammalian enzymes could have evolved by duplication and fusion of an ancestral 50 kDa hexokinase. Examples: hexokinase IV from human mitochondrial outer membrane: database code HXK1_HUMAN, 917 amino acids (102.39 kDa); the N-terminal and C-terminal halves of the sequence are similar; regulatory function of this monomeric allosteric enyme is associated with the N-terminal half; human brain hexokinase, type I: database code HXK1_HUMAN, 917 amino acids (102.39 kDa); human liver glucokinase isozyme (hexokinase D): database code HXKH_HUMAN, 466 amino acids (52.08 kDa); yeast hexokinase (3-D structure with glucose): database code NRL_1HKG, 457 amino acids (38.89 kDa); also, from yeast: database code HXKG_YEAST, 500 amino acids (55.31 kDa).

hexon a **capsomere** that is surrounded by six other capsomeres in an icosahedral virus capsid.

hexonic acid any monocarboxylic acid (i.e. aldonic acid) formally derived from a hexose by oxidation at C-1.

hexosamine any aminodeoxysugar with six carbon atoms.

hexosaminidase EC 3.2.1.52; *recommended name*: β-*N*-acetylhexosaminidase; *systematic name*: β-*N*-acetyl-D-hexosaminide *N*-acetylhexosaminohydrolase; *other name*: β-hexosaminidase. An enzyme that catalyses the hydrolysis of terminal nonreducing *N*-acetyl-D-hexosamine residues in *N*-acetyl-β-D-hexosaminides. It is a lysosomal enzyme in mammals; there are two precursors (human): α, database code HEXA_HUMAN, 529 amino acids (60.62 kDa); and β, database code HEXB_HUMAN, 556 amino acids (63.04 kDa). The α chain, a glycoprotein, comprises amino acids 109–529 of its precursor; three glycoproteins (all similar to α) are derived from the β precursor: β (amino acids 122–556), β-B (amino acids 122–311), and β-A (amino acids 315–556). There are three forms of the enzyme: form A, responsible for degradation of GM_2 gangliosides, is a trimer composed of one α chain, one β-A chain, and one β-B chain; form B is a tetramer of two β-A and two β-B chains; form S is a homodimer of two α chains. **Tay–Sachs dis-**

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ease is due to defects of the α chain and Sandoff disease due to defects of the β chain.

hexosan *a former name for* any of a class of polysaccharides that yield only hexoses on hydrolysis.

hexose any **aldose** having a chain of six carbon atoms in the molecule.

hexose diphosphate pathway *an alternative name for* **Embden–Meyerhof pathway**.

hexose monophosphate pathway *or* **hexose monophosphate shunt** *an alternative name for* **pentose phosphate pathway**.

hexose phosphate transport protein an integral membrane transport protein responsible for sugar phosphate uptake in bacteria. Example from *Escherichia coli*: database code UHPT_ECOLI, 463 amino acids (50.55 kDa).

hexose-1-phosphate uridylyltransferase *see* **UDP-glucose–hexose-1-phosphate uridylyltransferase**.

hexulose any **ketose** having a chain of six carbon atoms in the molecule.

hexuronic acid **1** any monocarboxylic acid (i.e. uronic acid) formally derived from a hexose by oxidation at C-6. **2** *a historical name originally used for* ascorbic acid.

hexyl *symbol*: Hx; the alkyl group, CH_3–$[CH_2]_4$–CH_2–, derived from hexane.

hexyl glucoside hexyl *β*-D-glucopyranoside; a mild nonionic detergent, CMC 250 mM.

Heyrovský, Jaroslav (1890–1967), Czech physical chemist; Nobel Laureate in Chemistry (1959) 'for his discovery and development of the polarographic methods of analysis'.

Hf *symbol for* hafnium.

HFBA *abbr. for* heptafluorobutyric acid; a reagent used in automatic peptide sequence analysis. It renders the action of cyanogen bromide specific to the cleavage of tryptophanyl peptide bonds.

HFCS *abbr. for* high fructose corn syrup.

Hfr *abbr. for* high-frequency recombinant.

HFT *abbr. for* high-frequency transduction.

Hg *symbol for* mercury.

HGF **1** *abbr. for* hepatocyte growth factor. **2** *abbr. for* hyperglycemic-glycogenolytic factor; *see* **glucagon**.

HGF receptor *see* **hepatocyte growth factor receptor**.

HGG *abbr. for* human gamma-globulin.

hGH *or* **HGH** *abbr. for* human growth hormone (i.e. human **somatotropin**).

HGPRT *abbr. for* hypoxanthine/guanine **phosphoribosyltransferase**; an enzyme that is important for the metabolic activation of purines, e.g. 6-mercaptopurine. Its deficiency is the cause of **Lesch–Nyhan syndrome**.

HHT *abbr. for* hydroxyheptadecatrienoic acid.

5-HIAA *abbr. for* 5-hydroxyindoleacetic acid.

hidden (immunological) determinant *or* **cryptodeterminant** any antigenic determinant so positioned that it is cryptic, i.e. normally not accessible for recognition by lymphocytes or antibody, but that becomes accessible after some stereochemical change occurs, e.g. by breakage, decomposition, or denaturation of the antigen. *See also* **cryptotope**.

hide the skin of an animal, especially the tough, thick skin of larger mammals. Powdered, dried hide is used in assays of some proteinases.

high-density lipoprotein *abbr.*: HDL; one of the classes of lipoproteins found in blood plasma in many animals (data normally relate to humans). They are also known as α lipoproteins, from having the highest electrophoretic mobility of the lipoproteins. HDL particles are the smallest of the blood lipoproteins: diameter 7.5–10 nm; solvent density for isolation 1.063–1.21 g mL^{-1}; hydrated density 1.21 g mL^{-1}. Their approximate composition (% by weight) is 6% unesterified cholesterol, 13% esterified cholesterol, 28% phospholipid, 3% triacylglycerol, 50% protein. Their apolipoprotein composition (% by weight total apolipoprotein) is 67% A-I, 22% A-II, 5–11% C-I + C-II + C-III, 1–2% E-II + E-III + E-IV, trace of D. They are synthesized in liver as precursor molecules, which undergo modification in plasma to the mature molecules, especially as a result of the action of **lecithin-cholesterol acyltransferase**. They appear to function in reverse transport of cholesterol from tissues to liver. *See also* **apolipoprotein** for individual apolipoproteins.

high-energy bond *symbol*: ~; *a term formerly sometimes used by biochemists for* a chemical bond whose hydrolysis is accompanied by an unusually large (>20 kJ mol^{-1}) negative standard free energy change. Although long used, the term has been recognized as incorrect and misleading, since it suggests that such a bond actually contains an unusually large amount of energy and fails to take into account the various factors that contribute to the large negative free energy change.

high-energy compound *a term formerly sometimes applied by biochemists to* any compound containing one or more so-called **high-energy bonds**, e.g. ATP, phospho*enol*pyruvate, acetyl-coenzyme A, etc.

high-frequency recombinant any bacterial strain that has a high frequency of recombination because the **F plasmid** has become incorporated into the bacterial chromosome. *See also* **Hfr**.

high-frequency transduction *abbr.*: HFT; any **transduction** in which the transducing phage(s) constitute a large proportion of the total phage population.

high-fructose corn syrup *abbr.*: HFCS; a mixture of fructose and glucose used as a sweetener in soft drinks, etc.; it is sometimes called **high fructose syrup** or, especially in Europe, **isoglucose**. The breakdown of corn starch to glucose (plus oligosaccharides) is followed by the action of **glucose isomerase** yielding a mixture consisting mainly of fructose and glucose. The product thus manifests the greater sweetness of fructose compared with glucose. The content is typically 42% fructose, 51% glucose, 5% maltose, and 2% other oligosaccharides.

highly conserved *see* **conserved**.

highly repetitive DNA a form of DNA that consists of short tandemly repeated sequences. It is found outside coding regions, and its role is unknown. Such DNA forms a significant proportion of most mammalian genomes.

high mobility group proteins *abbr.*: HMG proteins; small nuclear proteins that bind to nucleosomal DNA and probably maintain genes in a transcribable conformation. The name derives from their behaviour on electrophoresis. Example, HMG 14 from human: database code HG17_HUMAN, 89 amino acids (9.25 kDa).

high-performance capillary electrophoresis electrophoresis through a long coiled capillary column that gives very high resolution of e.g. peptides. *See also* **capillary electrophoresis**.

high-performance liquid affinity chromatography *abbr.*: HPLAC; a technique that combines the use of bioaffinity supports and **high-pressure liquid chromatography**.

high-performance liquid chromatography *abbr.*: HPLC; *an alternative name for* **high-pressure liquid chromatography**.

high-potential iron–sulfur protein *abbr.*: Hipip *or* HiPIP *or* HiPiP; a type of **ferredoxin**, originally found in the photosynthetic bacterium *Chromatium vinosum*, that has a very much higher redox potential ($E_o' \approx 0.3$ V) and different magnetic properties compared with other ferredoxins. The term has been used increasingly, but inappropriately, for other ferredoxins that, like the *Chromatium* protein, are able to form a higher than usual oxidation level but do not have high redox potentials.

high-pressure liquid chromatography *or* **high-performance liquid chromatography** *abbr.*: HPLC; a technique of **column chromatography** that is rapid and provides high resolution. It can be used with the various modes of liquid chromatography, the liquid being forced at high pressure, normally up to 420 kg cm^{-2} (6000 psi), through the column (which is usually of stainless steel) and thence through a detector into a fraction collector. Because of the ability to use high pressures, the particles of the support materials used for the stationary phase can be of very small diameter (3–10 μm), which greatly improves resolution.

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high-speed supernatant *a jargon term for* the supernatant resulting from high-speed centrifugation (≈100 000 *g*).

high-spin complex any of the complex transition-metal ions having a maximal number of unpaired electrons in the d- or f-shell. This state occurs when pairing energy is higher than the crystal field splitting energy. *Compare* **low-spin complex**.

high-voltage electron microscope a type of electron microscope that employs accelerating voltages of 1 Mev, ten times that of previous instruments, enabling images of thick sections and even intact cells to be produced without significant loss of resolution.

high-voltage electrophoresis *abbr.*: HVE; a technique of paper or thin-layer electrophoresis that results in better and more rapid separations (10–60 min) than the standard technique, which suffers from minimal diffusion of low-M_r components. The high-voltage technique employs currents of up to 500 mA and potential gradients of up to 200 V cm^{-1}. The high field strength requires cooling of the support and adequate protection devices to be incorporated into the apparatus.

Hildebrand solubility parameter *symbol*: δ; a measure of what is commonly called the polarity of a solvent; nonpolar solvents have low δ values while polar solvents have large values. In liquid–liquid chromatography the Hildebrand parameter indicates the relative position of a solvent in an eluotropic series. The parameter is the sum of a number of factors:

$$\delta = \delta_d + \delta_o + \delta_a + \delta_h,$$

where δ_d is a measure of interactions due to **dispersion forces**, δ_o is a measure of interactions due to dipole interactions, δ_a is a measure of the ability of the solvent to interact as a hydrogen acceptor, and δ_h is a measure of its interactions as a hydrogen donor. [After Joel Henry Hildebrand (1881–1983), US chemist.]

Hill **1 (Sir) Archibald Vivian Hill** (1886–1977), British physiologist and biophysicist; Nobel Laureate in Physiology or Medicine (1922) 'for his discovery relating to the production of heat in the muscle' [prize shared with O. F. Meyerhof]. **2 Robert ('Robin') Hill** (1899–1991), British plant biochemist noted for his studies of the mechanism of photosynthesis.

Hill coefficient *or* **Hill constant** *symbol*: h or n_H; *see* **Hill equation** and **Hill plot**.

Hill equation **1** an equation,

$$y = K[x]^h/(1 + K[x]^h),$$

used to express the binding of a ligand to a (macro)molecule. It may be rearranged to give:

$$\log[y/(1 - y)] = -\log K + h\log[x],$$

where y, the **fractional saturation**, is the fraction of the total number of binding sites occupied by ligand, $[x]$ is the free (unbound) ligand concentration, K is a constant, and h is the Hill coefficient. **2** *(in pharmacology)* an equation derived from the above relating the effect of a drug to its concentration. For an effect, E, produced when an agent, A, is applied at a concentration $[A]$, then the relationship between E and $[A]$ may often be described empirically by the equation

$$E/E_{max} = [A]^h/([A]_{50}{}^h + [A]^h),$$

where E_{max} is the maximal value of E and $[A]_{50}$ is the concentration that produces an effect that is 50% of E_{max}. [After A. V. Hill.]

Hill–Langmuir equation *(in pharmacology)* a variation of the **Langmuir absorption isotherm**; for a ligand, L, binding to a receptor, R, according to the equilibrium

$$L + R \overset{K_L}{\rightleftharpoons} LR,$$

$$p_{LR} = [L]/(K_L + [L]),$$

where p_{LR} is the fraction (proportion) of binding sites occupied by a ligand at equilibrium and K_L is the dissociation equilibrium constant.

Hill plot a plot of the **Hill equation** in the form $\log[y/(1 - y)]$ against $\log[x]$, where y is the fractional saturation with ligand and $[x]$ is the free (unbound) ligand concentration. The slope at any one point, h, is the Hill coefficient at that value of y. The values of h along the plot, which usually do not exceed the number of binding sites on each molecule and which tend to unity as y tends to 0 or 1, give an indication of the nature and degree of cooperativity (interaction) between the various binding sites on the molecule. [After A. V. Hill.]

Hill reaction the phenomenon in which isolated chloroplasts evolve dioxygen when illuminated in the presence of a suitable electron acceptor, e.g. ferricyanide or ferrioxalate, with a concomitant reduction of the electron acceptor. [After R. Hill.]

Hill reagent any electron acceptor that functions in a **Hill reaction**, e.g. ferrioxalate or ferricyanide.

hinge region **1** a flexible, proline-rich region of an **immunoglobulin** molecule, adjacent to the two disulfide bonds linking the two heavy chains together. It probably acts as a hinge on which the **Fab fragments** can rotate allowing the immunoglobulin molecule to take up a **Y**-shape when it reacts with antigen. The hinge region is near the sites of action of papain and pepsin. **2** the region in the helical, rod-shaped part of a **myosin** molecule that is susceptible to cleavage by trypsin to give light meromyosin and heavy meromyosin. **3** a region in any protein about which rigid body motions occur.

Hipip *or* **HiPIP** *or* **HiPiP** *abbr. for* high-potential iron–sulfur protein.

hippocalcin a neuron-specific Ca^{2+}-binding protein with **EF-hands**, similar to recoverin. It is expressed exclusively in the pyramidal layer of the hippocampus. Example from human: database code HIPP_HUMAN, 192 amino acids (22.30 kDa).

hirudin a dried extract obtained from leeches and possessing anticoagulant activity. The name is also applied to the purified active component, a 65-amino-acid polypeptide with three disulfide bridges; this has highly specific antithrombin properties, inactivating thrombin by blocking substrate-binding groups. Example from the leech *Hirudo medicinalis*: database code ITH1_HIRME, 65 amino acids (6.97 kDa).

hirudisin a recombinant **hirudin** variant engineered to inhibit α-thrombin and exhibit **disintegrin** activity. Hirudisins have antiplatelet aggregation activity. Replacement of the hirudin sequence Ser-Asp-Gly-Glu (residues 32–35) by Arg-Gly-Asp-Ser (RGDS) yields hirudisin, or by Lys-Gly-Asp-Ser yields hirudisin-1. The integrin-binding RGD motif of hirudisin is implicated in its antiplatelet action.

hirulog any synthetic peptide based on **hirudin** and designed as an inhibitor of the thrombin catalytic site, and exhibiting specificity for the anion-binding site of thrombin.

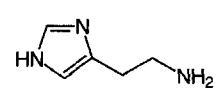
hirustasin an **antistasin**-like serine proteinase inhibitor isolated from the medicinal leech, *Hirudo medicinalis*.

His *symbol for* a residue of the α-amino acid L-**histidine** (alternative to H).

hist+ *a variant form of* **histo+** (before a vowel).

histaminase *see* **amine oxidase (copper-containing)**.

histamine 2-(4-imidazolyl)ethylamine; a compound formed by the decarboxylation of L-histidine and present in many mammalian tissues, with especially high concentrations in lung, skin, and intestine; it is stored in the granules of tissue mast cells and circulating basophil cells. Histamine is a potent vasodilator; it also increases capillary permeability, causes contraction of smooth muscle, plays a role in the regulation of gastric secretion, and acts as a mediator in allergic and anaphylactic conditions.



histamine receptor any of the receptors in mammalian tissues that interact specifically with **histamine**. Histamine receptors

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may be divided into three categories. **H1 receptors** mediate the stimulating effects of histamine on smooth muscle in the gut and bronchi and most of the depressor effects on blood pressure. They are antagonized (blocked) by such classical **antihistamines** as pyrilamine (mepyramine) and promethazine. The H_1 receptor has seven transmembrane domains coupled to the phosphatidylinositol-Ca^{2+} second messenger system. Example: database code HHIR_HUMAN, 487 amino acids (55.78 kDa). **H2 receptors** mediate the stimulation of gastric acid secretion, the increase in the contraction frequency of cardiac muscle, the increase in cyclic AMP stores in basophil and mast cells, the inhibition of release of histamine by mast cells, and the remaining depressor effects on blood pressure. They are antagonized by, e.g., **cimetidine**. In humans the H2 receptor has seven transmembrane domains, positively coupled to adenylate cyclase. Example: database code HH2R_HUMAN, 359 amino acids (40.1 kDa). **H3 receptors** have a receptor site characterized pharmacologically by radioligand binding; second messenger coupling and structure are unknown. They are associated with presynaptic nerve terminals and attenuate the release of neurotransmitters, e.g. histamine, acetylcholine, and norepinephrine. They are antagonized and blocked, e.g., by thioperamide and clobenpropit.

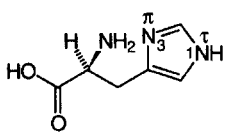
histidase *an alternative name for* **histidine ammonia-lyase**.

histidinal α-amino-β-4-imidazolepropionaldehyde; 2-amino-3-(1*H*-imidazol-4-yl)propanal; $(C_3H_3N_2)CH_2–CH(NH_2)–CHO$; the α-amino-aldehyde analogue of histidine. It is the immediate biosynthetic precursor of histidine.

histidinase *an alternative name for* **histidine ammonia-lyase**.

histidinate **1** histidine anion; the anion, $(C_3H_3N_2)CH_2–CH(NH_2)–COO^-$, derived from histidine. **2** any salt of histidine anion. **3** any ester of histidine.

histidine *the trivial name for* β-4-imidazolylalanine; α-amino-β-imidazole-4-propionic acid; 2-amino-3-(1*H*-imidazol-4-yl)propanoic acid; $(C_3H_3N_2)CH_2–CH(NH_2)–COOH$; a chiral α-amino acid. L-Histidine (*symbol*: H *or* His), (*S*)-2-amino-3-(1*H*-imidazol-4-yl)propanoic acid, is a coded amino acid found in peptide linkage in proteins; codon: CAC or CAU . It is also a component of the isopeptide **carnosine**. In mammals it is an essential dietary amino acid and is glucogenic. D-Histidine (*symbol*: D-His *or* DHis), (*R*)-2-amino-3-(1*H*-imidazol-4-yl)propanoic acid, is not known to occur naturally. N-1 and N-3 of the imidazole ring are designated τ and π respectively.



L-histidine

histidine ammonia-lyase EC 4.3.1.3; *systematic name*: L-histidine ammonia-lyase; *other names*: histidase; histidine α-deaminase; histidinase. An ammonia-lyase (deaminase) enzyme that catalyses the deamination of L-histidine to urocanate. It is widely distributed in animals, plants, and microorganisms; in plants it is present in **glyoxysomes**. The activity of this enzyme is defective in **histidinemia**.

histidine (base) a histidine residue in which the imidazole group is unprotonated.

histidine decarboxylase *abbr.*: HDC; EC 4.1.1.22; *systematic name*: L-histidine carboxy-lyase. A pyridoxal phosphate enzyme that catalyses the decarboxylation of L-histidine to histamine. It is similar to dopa and glutamate decarboxylases. Example from human (homodimer): database code DCHS_HUMAN, 662 amino acids (74.10 kDa).

histidinemia *or (esp. Brit.)* **histidinaemia** a rare, hereditary, human metabolic disorder in which abnormally high levels of histidine are found in the blood and urine. It is due to a defect in the activity of **histidine ammonia-lyase**.

histidine tail a sequence of (usually) about six histidine residues that is deliberately introduced at the C terminus of certain recombinant proteins. The purpose is to allow purification of the recombinant product by a type of affinity chromatography using a nickel chelating resin. Only the histidine-tailed proteins are retained by the column and these may then be eluted using a buffer containing imidazole.

histidinium **1** *a term normally used to mean* histidinium(1+); the (imidazolinium) monocation of histidine. In theory, the term denotes any ion or mixture of ions formed from histidine and having a net charge of +1, although the species $(C_3H_4N_2^+)CH_2–CH(NH_3^+)–COO^-$ generally predominates in practice. **2** *the systematic name for* histidinium(2+); the dication of histidine.

histidino **1** N^2-histidino; the alkylamino group, $(C_3H_3N_2)CH_2–CH(COOH)–NH–$, derived from histidine by loss of a hydrogen atom from its α-amino group. **2** either of the two possible groups, N^π-histidino or N^τ-histidino, $HOOC–CH(NH_2)–CH_2–(C_3H_2N_2)–$, derived from histidine by loss of a hydrogen atom from its position on one or other of the nitrogen atoms of the imidazole ring.

histidinol 4-(2-amino-3-hydroxypropyl)imidazole; 2-amino-3-(1*H*-imidazol-4-yl)propanol; $(C_3H_3N_2)CH_2–CH(NH_2)–CH_2OH$; the α-amino-alcohol analogue of histidine. It is an intermediate, together with its phosphate ester, in the biosynthesis of histidine, and a powerful reversible inhibitor of protein synthesis.

histidinol dehydrogenase *abbr.*: HDH; EC 1.1.1.23; L-histidinol:NAD^+ oxidoreductase. An enzyme that catalyses the oxidation of two molecules of NAD^+ of L-histidinol to L-histidine with reduction of the NAD^+ to NADH. Example from the *his* operon of *Salmonella typhimurium*: database code HISX_SALTY, 434 amino acids (45.85 kDa); the protein is a dimer and bifunctional as it also has an aldehyde dehydrogenase site, histidinol; being an intermediate. *See also* ***Salmonella* mutagenicity test**.

histidyl the acyl group, $(C_3H_3N_2)–CH_2–CH(NH_2)–CO–$, derived from histidine.

histo+ *or (before a vowel)* **hist+** *comb. form* denoting tissue.

histochemistry the chemistry of the tissues, as studied with a combination of the methods of chemistry and histology.

histocompatibility the extent to which an organism will tolerate a graft of a foreign tissue. —**histocompatible** *adj.*

histocompatibility antigen any of the genetically determined **isoantigens** present on the surface of many animal cells that determine the immune reactions to tissue grafts. If tissue is grafted onto a recipient of the same species that does not carry the same histocompatibility antigens as the graft material, an immune response may be provoked in the recipient leading to graft rejection. *See also* **HLA histocompatibility system**, **major histocompatibility complex**.

histocompatibility gene any gene determining the formation of a **histocompatibility antigen**. *See* **HLA histocompatibility system**, **major histocompatibility complex**.

histoelectrofocusing a technique in which an unfixed frozen section of tissue, 25–40 μm thick, is applied to a support gel and then subjected to **electrofocusing**. The proteins and enzymes present in the tissue move into the gel and may be revealed by staining or zymographic techniques.

histogram a diagram representing a frequency distribution. It consists of a number of contiguous rectangles whose widths are proportional to the class interval under consideration and whose heights are proportional to the frequency associated with each class.

histohematin *or (esp. Brit.)* **histohaematin** a term originally used (1884) by Charles Alexander MacMunn (1852–1911) for the pigments now known as **cytochromes**. It included **myohematin**.

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histone any of a group of evolutionarily highly conserved basic proteins, of molecular mass 11–21 kDa, that constitute about half the mass of the chromosomes of all eukaryotic cells, except spermatozoa. They comprise single polypeptide chains with a (lysine plus arginine) content of about 25%, and are concerned in the packing of DNA in **chromatin**. The principal histones may be classified into five types as shown in the table.

Type	Other names	Lys/Arg ratio	M_r	Location
H1	F1,Ia	20.0	21 000	linker
H2A	F2a2,IIb1	1.25	14 500	core
H2B	F2b,IIb2	2.25	13 800	core
H3	F3,III	0.72	15 300	core
H4	F2a1,IV	0.79	11 300	core

The octomer $(H2A,H2B,H3,H4)_2$ forms the **nucleosome** core. Examples from yeast: H2A.2, database code H2A2_YEAST, 131 amino acids (13.84 kDa); H2B.1, database code H2B1_YEAST, 130 amino acids (14.10 kDa); H3, database code H3_YEAST, 135 amino acids (15.21 kDa); H4, database code H4_YEAST, 102 amino acids (11.22 kDa). H1 is associated with nucleosomes, especially the linking DNA; example H1A (human): database code H1A_HUMAN, 222 amino acids (22.15 kDa). *See also* **H-NS**.

hitchhiking **1** *a jargon term for* the sequence of events in which a genetic element (or **transposon**) inserts into an active secondary site on a replicon which is then transferred to a recipient, the transposon then coming immediately to occupy its normal primary site in the DNA of the recipient organism. **2** the spread of a neutral allele through a population due to its linkage with a beneficial allele that is subject to selection.

Hitchings, George Herbert (1905–98), US biochemist and pharmacologist distinguished for his introduction, largely in collaboration with his colleague G. B. Elion, of a range of widely used synthetic drugs designed as antimetabolites, including the antifolate bactericidal agent co-trimoxazole, the immunosuppressants mercaptopurine and its derivative azathioprine, and the xanthine-oxidase inhibitor allopurinol; Nobel Laureate in Physiology or Medicine (1988) jointly with J. W. Black and G. B. Elion 'for their discoveries of important principles for drug treatment'.

HIV *abbr. for* human immunodeficiency virus; a **retrovirus**, the causative agent of **AIDS**. Two such viruses are known: HIV-1, found worldwide, and HIV-2, which is much less common, being found mainly in West Africa. In terms of the gene structure of the **viral envelope sequences** (*see* **HIV protein**) HIV-1 and HIV-2, although both members of the Lentivirus family of retroviruses, are not closely related. HIV-2 is closely related to a **simian immunodeficiency virus** (SIV) common in sooty mangabeys and probably originated there. HIV-1, which probably originated from a non-human primate in Africa, is closely related to SIV from chimpanzees. However, since the rate of SIV infection in chimpanzees is very low, it is not clear that they represent the natural host of these viruses. HIV is subclassified into eight alphabetical subtypes or clades, plus one orphan clade. The reverse transcriptase enzyme of HIV is highly error-prone, leading to a high mutation rate. Thus these viruses evolve very quickly even within single patients, and drug-resistant mutations appear rapidly. For HIV-1 to enter its target cells, it must not only bind to the cell-surface protein **CD4** but also to one or more chemokine receptors. One of these, named CCR5, is effective in the early stages of infection. Patients with defective CCR5 cannot be infected with HIV-1. During the later stages of infection, another chemokine receptor, CXCR4 (*former name*: fusin) dominates.

HIV-1 protease an aspartyl protease that is a homodimer of two subunits each containing 99 amino acids, with cysteines at positions 67 and 95. Its proteolytic function is essential for the life cycle of human immunodeficiency virus (HIV) and is, therefore, a target for the design of inhibitors as therapeutic drugs, several examples of which are in use.

HIV protein any of the proteins encoded by the human immunodeficiency virus (HIV). The HIV-1 genome (9.5 kb) is transcribed to give 12 different mRNAs generated by alternative splicing. The proteins are conventionally named for the gene and/or their size (kDa) with the convention that p = protein and gp = glycoprotein. The primary translation products are: Gag precursor (p53); Pol precursor; Env precursor (gp160); Nef (p27; negative regulator); Vif (p23); Tat (p14; regulatory protein); Rev (p19; regulatory protein); Vpr (p18); and Vpu (p15). The Gag precursor is cleaved to myristoylated Gag protein (p17), structural protein (p24), and p15; p15 is the precursor for RNA-binding protein (p7) and proline-rich protein (p9). The Pol precursor is cleaved to protease (p10), reverse transcriptase (p51), and endonuclease (p32). The Env precursor is cleaved to extracellular protein (gp120) and transmembrane protein (gp41). Protease, reverse transcriptase, and endonuclease are synthesized as part of a polyprotein: database code POL_HV1BR, 1015 amino acids (115.03 kDa). *See also* **retrovirus**.

HLA *abbr. for* human leukocyte-associated antigen. *See also* **histocompatibility antigen, major histocompatibility complex**.

HLA histocompatibility system a family of histocompatibility antigens encoded by the complex of genetic loci known as the **major histocompatibility complex** (MHC). It is the major histocompatibility system in humans, equivalent to the H-2 histocompatibility system in mice. The MHC genes control the presence of HLA **isoantigens** on cell surfaces. These antigens are of primary importance in tissue grafting since HLA-incompatible grafts are more likely to be rejected than incompatible grafts of other isoantigen groups.

HLH *abbr. for* helix-loop-helix (*see* **helix-turn-helix**).

***hly* genes** *see* **hemolysin**.

HMC *abbr. for* 5-hydroxymethylcytosine.

H-meromyosin *abbr. for* heavy meromyosin.

hMG *or* **HMG** *abbr. for* human menopausal gonadotropin (i.e. human urogonadotropin).

HMG **1** *abbr. for* 2-hydroxy-2-methylglutaryl. **2** *abbr. for* high mobility group of nuclear proteins. **3** *see* **hMG**.

HMG-CoA *abbr. for* hydroxymethylglutaryl-CoA.

HMG-CoA lyase *abbr. for* hydroxymethylglutaryl-CoA lyase.

HMG-CoA reductase *abbr. for* hydroxymethylglutaryl-CoA reductase.

HMG-CoA synthase *abbr. for* hydroxymethylglutaryl-CoA synthase.

HMM *abbr. for* heavy meromyosin.

HMMA *abbr. for* hydroxymethoxymandelate.

HMP *abbr. for* hexose monophosphate.

HMP pathway *or* **HMP shunt** *abbr. for* hexose monophosphate pathway (shunt) (i.e. **pentose phosphate pathway**).

HNPCC a human gene that may normally function in the repair of regions of mismatch of DNA. It is named from hereditary nonpolyposis colorectal cancer, a condition associated with mutations in this gene.

hnRNA *or* **HnRNA** *abbr. for* heterogeneous nuclear RNA (alternatives to H-RNA).

hnRNP *abbr. for* heterogeneous nuclear ribonucleoprotein.

hnRNP particles *abbr. for* heterogeneous nuclear ribonucleoprotein particles; particles in the nucleus containing **hnRNA** bound to protein.

H-NS bacterial proteins of several families that are basic DNA-binding proteins, possibly the prokaryotic counterparts of **histones** in eukaryotic chromatin. Their role remains unclear. They have the ability to bind to curved DNA and may have a role in transcriptional regulation. The N-terminal tetrapeptide, consensus Ser-Glu-Xaa-Leu, is characteristic. Example from *Escherichia coli*: protein H1, dimer, database code HNS_ECOLI, 136 amino acids (15.39 kDa). The name derives from an isolation procedure extracting them from the 30S ribosomal native subunit.

Ho *symbol for* holmium.

Hodgkin **1 (Sir) Alan Lloyd** (1914–98) British physiologist

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renowned for his researches on nerve-impulse conduction; Nobel Laureate in Physiology or Medicine (1963) jointly with J. C. Eccles and A. F. Huxley 'for their discoveries concerning the ionic mechanisms involved in excitation and inhibition in the peripheral and central portions of the nerve cells membrane'. **2 Dorothy (Mary) Crowfoot-Hodgkin** *née* Crowfoot, (1910–94), British chemist and crystallographer renowned for her elucidation by X-ray crystallography of the molecular structures of benzylpenicillin (formerly termed penicillin G) and cyanocobalamin (a version of vitamin B_{12}) and in particular of the complete three-dimensional structure of crystalline zinc insulin (announced in 1969, having – as D. M. Crowfoot – first observed its diffraction pattern in 1934); Nobel Laureate in Chemistry (1964) 'for her determination by X-ray techniques of the structures of important biochemical substances', e.g. penicillin, vitamin B_{12}, and insulin.

Hoechst 33258 *see* **bisbenzimide**.

Hoechst 33342 *see* **bisbenzimide**.

Hoff *see* **van't Hoff**.

Hofmeister series *or* **lyotropic series** an arrangement of either the simple anions or the simple cations (or of the salts of such ions) in order of their ability to remove lyophilic substances from colloidal solutions. Each series is an index of, *inter alia*, the relative abilities of the ions to salt-out proteins from solution. The order for anions is: $citrate^{3-} > tartrate^{2-} > acetate^{-} > NO_3^- > ClO_4^- > CNS^-$, and that for cations is: $Mg^{2+} > Ca^{2+} > Sr^{2+} > Ba^{2+} > Li^+ > Na^+ > K^+ > Rb^+ > Cs^+$. [After Franz Hofmeister (1850–1922).]

Hofstee plot *see* **Eadie–Hofstee plot**.

Hogness box *an alternative name for* **TATA box**.

hol+ *a variant form of* (before a vowel) **holo+**.

holandric inherited solely in the male line. *Compare* **hologynic**.

holdback agent *or* **holdback carrier** any nonradioactive substance that is added to a sample to prevent either coprecipitation or adsorption of some soluble radioactive substance.

hold-up volume *symbol*: V_M; *(in chromatography)* the volume of eluent required to elute a component whose concentration in the stationary phase is negligible relative to that in the mobile phase. In gas chromatography, the volume of carrier gas (eluent) is specified at the same temperature and pressure as the total retention volume.

hole *(in physics)* the absence of an electron in a normally filled valency structure of a crystalline **semiconductor** that behaves as a carrier of charge and is mathematically equivalent to a positron.

Holley, Robert William (1922–93), US biochemist and molecular biologist noted for his establishment of the structure of alanine transfer RNA, this being the first occasion on which the sequence of a nucleic acid had been determined; Nobel Laureate jointly with H. G. Khorana and M. W. Nirenberg (1968) for their 'interpretation of the genetic code and its function in protein synthesis'.

Holliday junction *or* **Holliday structure** one of the junctions between four strands of DNA that are important intermediates in **genetic recombination**. They are part of the mechanism for **crossing over** during the long prophase of meiotic cell division I, when four strands of DNA are aligned. The process involves breaking the DNA double helix in a maternal chromatid and in a homologous paternal chromatid and then exchanging fragments between the two non-sister chromatids in a reciprocal fashion. At this point, in each four strands, a paternal strand links across to a maternal strand, forming the junction known by the name of its proposer. [After Robin Holliday (1932–), British biologist.]

hollow-cathode discharge lamp a radiation source used in **atomic absorption spectrophotometry** to produce a spectrum of radiation specific to the element being assayed. A sample of the element in question is held in a metal cup-shaped cathode, which, together with a tungsten anode, is enclosed in a glass or quartz envelope filled with argon at low pressure. A high voltage is used to produce an arc spectrum of the element.

hollow-fibre technique a technique in which bundles of semipermeable, hollow fibres with pores of controlled dimensions that function as molecular sieves are used for concentrating, desalting, dialysing, and fractionating macromolecules in solution. *Compare* **capillary filtration**.

holo+ *or (before a vowel)* **hol+** *comb. form* whole, entire, complete; wholly, entirely, completely.

holocellulose the complex mixture of polysaccharides remaining after the removal of lignin from tree-wood by treatment with sodium chlorite solution. It consists of a mixture of **cellulose** and **hemicellulose**.

holocrine **1** describing a type of secretion that involves disintegration of the entire secretory cell to release the secretory products. **2** describing a gland made up of such cells. *Compare* **apocrine**, **eccrine**, **merocrine**.

holoenzyme a catalytically active complex comprising the protein part of an enzyme (**apoenzyme**) combined with the appropriate cofactor or cofactors.

hologram **1** the pattern produced when light, or other electromagnetic radiation, that has been reflected, diffracted, or transmitted by an object placed in a coherent beam, interferes with a reference beam related in phase to the first beam. **2** a photograph of such a pattern.

holograph **1** to make a **hologram** (def. 1, 2). **2** any book or other document handwritten by its author.

holography the process of making and using **holograms** (def. 1, 2). —**holographic** *adj.*

hologynic inherited solely in the female line. *Compare* **holandric**.

Holometabola *or* **Endopterygota** one of the two divisions of the subclass Pterygota, comprising those insects, e.g. butterflies, moths, flies, and beetles, in which the juvenile forms (larvae) are very different from the adults. Such insects undergo complete metamorphosis during a resting stage (pupa). *Compare* **Hemimetabola**.

holoprotein the functional form of a protein containing a protein part (**apoprotein**) together with any appropriate ligand or ligands.

holorepressor a functional repressor protein consisting of an **aporepressor** plus **corepressor** complex.

homeo+ *or* **homoeo+** *or* **homoio+** *comb. form* denoting like or similar.

homeobox a short (180 bp) conserved DNA sequence that encodes a DNA-binding motif famous for its presence in genes that are involved in orchestrating the development of a wide range of organisms. *See also* **homeotic gene**.

homeodomain the DNA-binding motif of 60 amino acids encoded by a **homeobox**.

homeomorphism *or* **homoeomorphism** *(in chemistry)* the property shown by certain substances of having the same crystal form but different compositions. —**homeomorphic, homeomorphous**, *or* **homoeomorphic, homoeomorphous** *adj.*

homeostasis *or* **homoeostasis** the maintenance of a relatively constant internal environment in the bodies of higher animals by means of a series of interacting physiological and biochemical processes. —**homeostatic** *or* **homoeostatic** *adj.*

homeotic gene *or* **homeodomain-encoding gene** *or* **homeobox-encoding gene** *or* ***Hox* gene**; any of the genes that are allelic for mutations resulting in the conversion of one body part into another. Homeotic genes were first discovered in *Drosophila*; a mutation in such a gene could, e.g., result in a leg replacing an antenna. While *Drosophila* has only two *Hox* clusters, in nematodes there is one, and in vertebrates four clusters of 9 to 11 genes each located on a separate chromosome and spanning more than 100 kb. The vertebrate *Hox* genes are expressed in specific patterns and at particular stages in embryogenesis. They are activated by **retinoic acid** and **sonic hedgehog protein**. In the limb these are active in concert with **fibroblast growth factor**. The degree of homology of the *Hox* genes in different species is remarkably high. The structure of some homeodomains has been determined, as has their interaction with DNA.

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homeothermic *the usual US spelling of* **homoiothermic**.

homeotypic pertaining to, or being the second, reductive division in **meiosis**. *Compare* **heterotypic**.

homo+ *comb. form* **1** the same, similar, alike. *Compare* **allo+** (def. 1); **hetero+** (def. 1); **iso+** (def. 1); **xeno+** (def. 1). **2** from, or directed towards, the same species. *Compare* **allo+** (def. 2); **hetero+** (def. 2); **iso+** (def. 2); **xeno+** (def. 2). **3** containing atoms, groups, linkages, residues, or subunits of the same kind. *Compare* **hetero+** (def. 3). **4** denoting the next higher homologue of a specified chemical compound, especially one whose molecules contain, in a hydrocarbon chain or ring, one more methylene, $-CH_2-$, than those of of the parent compound, e.g. homocysteine, homoserine, homo-5α-pregnane. *Compare* **nor+** (def. 2).

Homo a genus of primates that includes modern man (*Homo sapiens*) and a number of more primitive, fossil species.

homoarginine *(sometimes) a trivial name for* N^6-amidino lysine.

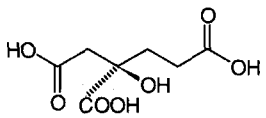
homobifunctional describing a chemical reagent that carries two identical reactive groups. *Compare* **heterobifunctional**.

homocarnosine *(sometimes) a trivial name for* N^{α}-(4-aminobutyryl)histidine.

homochromatic *a less common term for* **monochromatic** (def. 1).

homochromatography a chromatographic technique for the separation of labelled oligonucleotides, in which a mixture of unlabelled oligonucleotides is used to displace the labelled components according to differences in size.

homocitrate 2-hydroxybutane-1,2,4-tricarboxylate; the (*R*) enantiomer is a component of the **aminoadipic pathway** and is formed by **homocitrate synthase**.

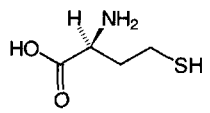


homocitrate synthase EC 4.1.3.21; *systematic name*: 2-hydroxybutane-1,2,4-tricarboxylate 2-oxoglutarate-lyase (CoA-acetylating). An enzyme that catalyses the formation of **homocitrate** from 2-oxoglutarate and acetyl-CoA and H_2O. *See also* **aminoadipic pathway**.

homoconjugation the association between a base and its conjugate acid through a hydrogen bond. *See* **conjugate acid–base pair**. *Compare* **heteroconjugation**.

homocyclic **1** describing any cyclic molecular structure containing atoms of a single element in the ring or rings; describing any compound having such a structure. The term is preferred to its synonym **isocyclic**; it includes **carbocyclic** (def. 1). *Compare* **heterocyclic** (def. 1). **2** any such compound.

homocysteine *symbol*: Hcy; α-amino-γ-mercaptobutyric acid; 2-amino-4-mercaptobutanoic acid; an important intermediate in the metabolic reactions of its *S*-methyl derivative, methionine. Its concentration in human serum is raised after stroke.



L-homocysteine

homocysteine methyltransferase one of several enzymes, e.g. the two alternative forms of enzyme synthesizing methionine: (1) 5-methyltetrahydrofolate–homocysteine *S*-methyltransferase. (EC 2.1.1.13); *other name*: tetrahydropteroylglutamate methyltransferase; it catalyses a reaction between 5-methyltetrahydrofolate and L-homocysteine to form tetrahydrofolate and L-methionine; cobalamin is a cofactor. Example, *metH* gene product in *Escherichia coli*: database code METH_ECOLI, 1226 amino acids (135.81 kDa). (2) 5-methyltetrahydropteroyltriglutamate–homocysteine *S*-methyltransferase (EC 2.1.1.14); *other name*: tetrahydropteroyltriglutamate methyltransferase; it catalyses a reaction between 5-methyltetrahydropteroyltri-L-glutamate and L-homocysteine to form tetrahydropteroyltri-L-glutamate and L-methionine. Example, *metE* gene product in *E. coli*: database code METE_ECOLI, 752 amino acids (84.91 kDa).

homocystine 2,2′-diamino-4,4′-dithiobis(butanoic acid); the disulfide oxidation product of **homocysteine**.

homocystinemia *or (esp. Brit.)* **homocystinaemia** inherited biochemical abnormality of humans, characterized by an abnormally high concentration of homocystine in the blood; this may be accompanied by a corresponding elevation of homocystine in the urine (**homocystinuria**); alternatively, homocystinuria may be the chief presenting sign. Either condition may be due to either: (1) a deficiency of cystathionine β-synthase (EC 4.2.1.22) activity (the deficiency preventing the condensation of homocysteine with serine to form cystathionine); or (2) a deficiency of the 5-methyltetrahydrofolate-dependent pathway for the remethylation of homocysteine to methionine.

homodetic describing a cyclic peptide in which the ring consists solely of amino-acid residues in eupeptide linkage. *Compare* **heterodetic**.

homodimer any macromolecular structure in which two identical subunits (monomers or protomers) are noncovalently associated. *See also* **dimer**. *Compare* **heterodimer**.

homoduplex hybrid DNA involving two strands that are complementary. *Compare* **heteroduplex**.

homoeo+ *a variant form of* **homeo+**.

homogametic describing the sex whose cell nuclei contain a pair of similar **sex chromosomes**. The homogametic sex is usually female, but is male in the Lepidoptera, birds, some amphibians and fishes, and a few plants. *Compare* **heterogametic**.

homogenate any disrupted tissue preparation in which cell disruption is maximal while the destruction of intracellular organelles is kept to the minimum.

homogeneic *an alternative term for* **allogeneic**. *Compare* **heterogeneic**.

homogeneous **1** being uniform in kind, as in a homogeneous population. **2** *(describing a group of molecules)* uniform in structure or composition. **3** *(describing a system)* consisting of only a single chemical phase. *Compare* **heterogeneous**, **homogenous**. **—homogeneity** *n.*

homogeneous catalysis any catalytic action or process in which the catalyst is uniformly distributed in the same chemical phase as the reactants. *Compare* **heterogeneous catalysis**.

homogeneous enzyme immunoassay *or* **enzyme-multiplied immunoassay technique** (*abbr.*: EMIT) a technique of **homogeneous immunoassay** in which an enzyme is covalently coupled to the substance to be assayed. The enzymic activity of the complex is inhibited by an antiserum specific for the substance and this inhibition is relieved by the presence of free molecules of the substance to be assayed. The enzyme acts as a molecular amplifier.

homogeneous immunoassay any **immunoassay** that does not involve physical separation of antibody-bound antigen from antigen molecules that remain free. Labels that may be attached to the antigen include: enzymes, cofactors, prosthetic groups or substrates of enzymes, chemiluminescent or fluorescent molecules, stable free radicals. *Compare* **heterogeneous immunoassay**.

homogeneously staining region a region in a chromosome that stains homogeneously, rather than with the banding pattern normally seen. The region contains massively amplified numbers of copies of a small segment of the genome. The amplified DNA may often consist of multidrug resistance gene DNA (*see* **MDR**).

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homogenesis the production of offspring having the same characteristics in successive generations. *Compare* **heterogenesis**.

homogenetic describing chromosome pairing during meiosis when the pairing partners are derived from one of the original ancestors. *Compare* **heterogenetic**.

homogenic *or* **congenic** **1** describing a gamete that contains only one allele of a particular gene. **2** describing two genetic elements that are descended from a common ancestor by a known sequence of steps. **3** *an alternative word for* **homogeneous**. *Compare* **heterogenic**.

homogenize *or* **homogenise** produce a **homogenate**. —**homogenization** *or* **homogenisation** *n.*

homogenizer *or* **homogeniser** any apparatus for producing a **homogenate**.

homogenous **1** of, pertaining to, or exhibiting **homogeny**. **2** *an alternative word for* **homogeneous**.

homogentisate *or (formerly)* **alcapton** 2,5-dihydroxyphenylacetate; an intermediate in the catabolism of tyrosine and in the biosynthesis of plastoquinone and tocopherol. It is excreted in abnormally large quantities in the urine in **alcaptonuria**. *See also* **homogentisate 1,2-dioxygenase**.

homogentisate 1,2-dioxygenase EC 1.13.11.5; *systematic name*: homogentisate:oxygen 1,2-oxidoreductase (decyclizing); *other names*: homogentisicase; homogentisate oxygenase; homogentisic acid oxidase. An enzyme that catalyses the oxidation by dioxygen of homogentisate to 4-maleylacetoacetate; iron(II) is a cofactor. In the catabolism of L-tyrosine, **homogentisate** is formed from 4-hydroxyphenylpyruvate; maleylacetoacetate is converted to fumarylacetoacetate, which is split to fumarate and acetoacetate.

homogeny *(in biology)* similarity in the structure of organisms or parts of organisms because of common ancestry.

homoglycan *or* **homopolysaccharide** any polysaccharide (i.e. glycan) that contains residues of only one kind of monosaccharide (i.e. glycose) molecule. *Compare* **heteroglycan**.

homograft *an old term for* **allograft**. *Compare* **heterograft**.

homoio+ *a variant form of* **homeo+**.

homoiosmotic describing organisms with a constant internal osmotic pressure. *Compare* **poikilosmotic**.

homoiothermic *or* **homoiothermal** *or (esp. US)* **homeothermic** *or* **homeothermal** describing an organism (**poikilotherm**) that sustains a relatively constant body temperature, usually higher than that of its surroundings. *Compare* **poikilothermic**. —**homoiothermy** *or (esp. US)* **homeothermy** *n.*

homokaryon *or* **homocaryon** any cell with more than one nucleus, and in which the nuclei are all of the same genetic constitution; a tissue composed of such cells. *Compare* **heterokaryon**. —**homokaryotic** *or* **homocaryotic** *adj.*

homokaryosis *or* **homocaryosis** the condition of having a **homokaryon** or homokaryons. *Compare* **heterokaryosis**.

homolactic fermentation a type of fermentation of glucose to lactate via the **Embden–Meyerhof pathway**. *Compare* **heterolactic fermentation**.

homolog *(sometimes) the US spelling of* **homologue**.

homologous **1** having a related or similar position, structure, etc.; corresponding; exhibiting **homology**. **2** *(in chemistry)* describing compounds that form a series with successive constant differences in composition. **3** *(in biology)* of common ancestry; especially of organs and tissues that have a similar anatomical position and structure in different species by virtue of their common evolutionary origin, even though their functions may have come to differ; e.g. the wing of a bird and the forelimb of a reptile. *Compare* **analogous**. **4** *(in genetics)* describing chromosomes that pair during meiosis, each member of a homologous pair being a duplicate of one of the chromosomes contributed at syngamy by the mother or the father. **5** *(in biochemistry)* **a** (of sequences of residues in encoded macromolecules) having the same or similar residues at corresponding positions (*see also* **conserved**). With respect to proteins the term is used to imply a common evolutionary origin. Specifically this requires evidence based on gene structure and not merely a similarity of protein structure. **b** (of proteins from different species) having identical or similar functions. *Compare* **heterologous**. —**homology** *n.*

homologous antibody the antibody elicited by a specified antigen.

homologous antigen the antigen that has elicited a specified antibody.

homologous desensitization *see* **desensitization**.

homologue *or (sometimes) US* **homolog** **1** (something) exhibiting homology. **2** *(in chemistry)* any member of a **homologous** (def. 2) series of compounds. **3** *(in biology)* any one of a series of **homologous** (def. 3) organs or structures. **4** *(in genetics)* **a** either members of a pair of **homologous** (def. 4) chromosomes. **b** either one of two genes in corresponding loci in homologous chromosomes.

homology domain any of the regions in an immunoglobulin involved in forming the **immunoglobulin fold**.

homolysis *(in chemistry)* the cleavage of a covalent bond in such a manner that each of the fragments between which the bond is broken retains one of the bonding electrons; e.g. A–B → A· + B·. —**homolytic** *adj.*

homooligomer any **oligomer** made up of only one kind of constitutional repeating unit. —**homooligomeric** *adj.*

homophilic binding *(of adhesion molecules)* binding of an adhesion molecule in one cell to an identical molecule in an adjacent cell. *Compare* **heterophilic binding**.

homopolymer any polymer made up of only one kind of constitutional repeating unit. For example, cellulose contains only glucose as the monomeric unit. —**homopolymeric** *adj.*

homopolymer tailing *a jargon term for* a procedure useful in joining two types of duplex DNA molecules to form mixed dimeric circular DNA. In this procedure, homopolymer sequences of one type, e.g. poly(dA), are added to the 3′-ends of one of the populations of DNA molecules, while complementary homopolymer sequences, e.g. poly(dT), are added to the 3′-ends of the other population of DNA molecules. The two types of molecules are then annealed to form mixed dimeric circles.

homopolysaccharide *an alternative name for* **homoglycan**.

homoserine *symbol*: Hse; α-amino-γ-hydroxybutyric acid; an intermediate in the biosynthesis of cystathionine, threonine, and methionine. It also occurs in bacterial peptidoglycans and, as its *O*-guanidino derivative, in canavanine. The term normally implies the L enantiomer.

homoserine deaminase *see* **cystathionine γ-lyase**.

homoserine dehydratase *see* **cystathionine γ-lyase**.

homoserine dehydrogenase EC 1.1.1.3; *systematic name*: L-homoserine:NAD(P)$^+$ oxidoreductase; an enzyme of the pathways for the biosynthesis of methionine and threonine. It catalyses the formation of L-homoserine and NAD(P)$^+$ from L-aspartate 4-semialdehyde and NAD(P)H. Example, a homotetrameric bifunctional enzyme from *Escherichia coli*: database code AK1H_ECOLI, 820 amino acids (89.02 kDa). Amino acids 1–249 form the aspartokinase I domain, amino acids 250–470 form a large 'interface', and 471–820 form homoserine dehydrogenase; regulation is by L-Thr. Another example is from *Corynebacterium glutamicum* and *Brevibacterium lactofermentum*: database code DHOM_CORGL, 445 amino acids (46.39 kDa). *See also* **aspartokinase/homoserine dehydrogenase**.

homoserine lactone *symbol*: Hsl; α-amino-γ-butyrolactone; a substance formed by the cleavage of methionine-containing peptides by cyanogen bromide.

homosterism *or* **homostery** the phenomenon in which a second molecule of normal substrate, or a structurally similar compound, combines at the catalytic site of an enzyme leading to a modification in the reaction of the bound intermediate. *Compare* **allosterism**. —**homosteric** *adj.*

homostery *an alternative term for* **homosterism**.

homothallic describing species, e.g. of certain fungi and algae, in which a sexual spore can result from the fusion of nuclei that are genetically distinct (i.e. not necessarily homozygous), but are derived from the same thallus; thus the species is self-fertile.

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homothallic switching endonuclease a sequence-specific endonuclease, with a site on yeast chromosome III, that is involved in mating-type switching. It is a **zinc finger** protein. Database code HO_YEAST, 586 amino acids (66.06 kDa).

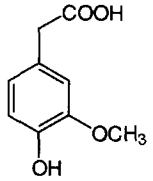
homotherm *an alternative word for* **homoiotherm**.

homotope any residue that can take the place of another residue in a particular position in a polymer; e.g. the serine and glycine residues at position 9 of the A chain of bovine and ovine insulin, respectively, are homotopes.

homotransplant **1** *an alternative term for* **homograft**. **2** to effect such a transplant.

homotropic describing an **allosteric** effect in which interaction occurs between identical ligands; the effect appears to be always cooperative. The term is applied also to such an interaction in the case of an allosteric enzyme for which the same substance acts as both the substrate and the allosteric effector, etc. *Compare* **heterotropic** (def. 1).

homovanillic acid 4-hydroxy-3-methoxyphenylacetic acid; a metabolite of catecholamine metabolism, found in human urine. It is the principal urinary metabolite of dopa and dopamine. It is used as a reagent in the fluorometric determination of glucose oxidase and other oxidases.



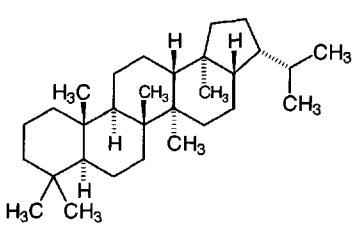
homozygosis **1** the union of gametes identical for one or more pairs of genes to form a **homozygote**. **2** *or* **homozygosity** the state or condition of being a homozygote. *Compare* **heterozygosis**.

homozygosity *an alternative term for* **homozygosis** (def. 2).

homozygote any cell or organism having identical genes (alleles) at one or more corresponding loci on homologous chromosomes. With respect to such loci, a homozygote will produce two identical gametes. *Compare* **heterozygote**. — **homozygotic** *or* **homozygous** *adj.*

Hoogsteen base pair a nucleic-acid base pair that differs from the Watson–Crick base pair. In the Hoogsteen adenine–thymine base pair the 6-NH_2 and N-7 of the adenine are hydrogen bonded respectively to the 4-O and H-1 of the thymine. The Hoogsteen guanine–cytosine pair requires that N-1 of the cytosine is protonated. In this base pair the 6-O and N-7 of the guanine are hydrogen bonded respectively to the 4-NH_2 and the protonated N-1 of cytosine. In Watson–Crick base pairs the glycosidic bond of both nucleotides has the *anti* conformation, but in the Hoogsteen pairs the glycosidic bond of the purine nucleotide has the *syn* conformation. Hoogsteen base pairs are particularly important in the structure of DNA triple helices, where the third strand forms Hoogsteen pairs to bases in the DNA duplex. [After Karst Hoogsteen (1923–), Dutch–American biochemist, who first described it.]

hopane the pentacyclic triterpene hydrocarbon parent of hopanone and derivatives found in plant resins. *See also* **hopanoids**.

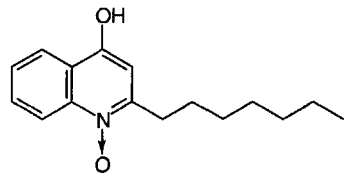


hopanoids pentacyclic sterol-like molecules based on the **hopane** nucleus. They are found in bacteria, some plants and lichens, and in sediments and crude oils, and are said to be the most abundant organic molecules in the biosphere (estimated total biomass 10^{11} to 10^{12} tonnes), thus outranking **cellulose**.

Hopkins, (Sir) Frederick Gowland (1861–1947), British biochemist renowned for his discoveries of essential amino acids and accessory food factors (later termed vitamins), for his isolation of glutathione and tryptophan, and for playing an important part in establishing biochemistry as an independent discipline; Nobel Laureate in Physiology or Medicine (1929) 'for his discovery of the growth-stimulating vitamins' [prize shared with Christiaan Eijkman].

Hopkins–Cole reaction a colour reaction for free or combined tryptophan, in which a violet colour is produced when a solution containing tryptophan is treated with glyoxylic acid (present in impure glacial acetic acid) and subsequently layered onto a solution of pure, concentrated sulfuric acid. [After F. G. **Hopkins** and Sydney William Cole (1877–1951).]

HOQNO *or* **HQNO** *abbr. for* 2-*n*-heptyl-4-hydroxyquinoline *N*-oxide; an inhibitor of the mitochondrial respiratory chain at cytochrome bc_1 and of photosynthetic electron flow immediately before cytochrome b_{559}LP.



hordein a type of **glutelin** found in barley.

hormone any substance formed in very small amounts in one specialized organ or group of cells and carried (sometimes in the bloodstream) to another organ or group of cells, in the same organism, upon which it has a specific regulatory action; an **endocrine** (def. 2). The term was originally applied to agents with a stimulatory physiological action in vertebrate animals (as opposed to a **chalone**, which has a depressant action). Usage is now extended to regulatory compounds in lower animals and plants, and to synthetic substances having comparable effects. *Compare* **autacoid**, **hermone**. *See also* **secretin**. —**hormonal** *adj.*

hormone cascade *see* **cascade sequence**.

hormone-sensitive lipase any enzyme of the sub-subclass EC 3.1.1 that, when activated in adipose tissue, catalyses the mobilization of fatty acids into the circulation. Such enzymes are activated by cyclic AMP-dependent phosphorylation under the influence of catecholamines, and are inactivated by insulin-dependent dephosphorylation. Example from human: database code LIPS_HUMAN, 786 amino acids (85.38 kDa).

hormonotoxin any conjugate of a peptide hormone and a peptide toxin, e.g. ovine luteinizing hormone–gelonin.

host **1** any organism in which another organism, especially a **parasite** or **symbiont**, spends part or all of its life cycle and from which it obtains nourishment and/or protection. **2** any organism that harbours a pathogenic or nonpathogenic infectious agent. **3** the recipient of a transplanted tissue or organ graft. **4** a cell or organism that contains recombinant DNA.

host cell any cell whose metabolism is used for the growth and reproduction of a virus.

host-cell reactivation *abbr.*: HCR; the restoration of activity in a UV-damaged DNA bacteriophage by the excision-repair mechanisms of the host cell in which it multiplies.

host-controlled modification *or* **host-controlled variation** *or* **host-induced modification** *or* **host-induced variation** any non-heritable change in the properties of a DNA bacteriophage re-

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sulting from the phage DNA assuming the DNA **modification** pattern characteristic of the host bacterium. It is usually recognized by **restriction** in the efficiency of plating of the newly modified phage on its former host strain. Similar phenomena have been described for viruses infecting eukaryotic cells.

host-induced modification *or* **host-induced variation** *see* **host-controlled modification**.

host range the spectrum of host organisms that can be infected by a specified infectious agent or parasite.

host–vector system a compatible combination of host and **vector** (def. 3) that allows propagation of DNA.

hot *(in physics) an informal term* describing a substance or material that contains a radionuclide, especially if **carrier-free** or at a dangerously high activity or specific activity. *Compare* **cold**.

hot laboratory *or* **hot lab** *an informal term for* a laboratory reserved and equipped for the manipulation of radioactive substances or materials of (dangerously) high activity.

hot room **1** a room (or laboratory) maintained at a constant, higher-than-ambient temperature. **2** *an informal term for* a room (or laboratory) that is specially equipped to deal with high levels of radioactivity.

hot spot any site at which mutations are observed with an unusually high frequency. Such sites have a highly enhanced, inherent susceptibility to mutation that cannot be ascribed to the type of base pair involved, the way in which it is altered, or the resulting change in any protein encoded by the DNA molecule.

hour *symbol*: h *or* hr; a non-SI unit of time equal to 3600 s.

housekeeping genes *see* **constitutive genes**.

Houssay, Bernardo Alberto (1887–1971), Argentinian physiologist and endocrinologist noted for his researches on diabetes and on the internal secretions of the adrenal, anterior pituitary, and thyroid glands; Nobel Laureate in Physiology or Medicine (1947) 'for his discovery of the part played by the hormone of the anterior pituitary lobe in the metabolism of sugar' [prize shared with C. F. and G. T. Cori].

Houssay animal a pancreatectomized animal which has also undergone **hypophysectomy**. The latter ameliorates the diabetic state that results from pancreatectomy by abolishing the secretion of **somatropin**. [After B. A. **Houssay**.]

***Hox* gene** *see* **homeotic gene**.

Hp **1** *symbol for* the heptyl group, CH_3–$[CH_2]_5$–CH_2–. **2** *abbr. for* haptoglobin.

HP-1 *abbr. for* helper peak-1 (now called **interleukin 1**).

HPCE *abbr. for* high performance capillary electrophoresis.

HpETE *abbr. for* hydroperoxyeicosatetraenoate.

hPL *or* **HPL** *abbr. for* human placental lactogen.

HPLAC *abbr. for* high-performance liquid affinity chromatography.

HPLC *abbr. for* high-pressure liquid chromatography *or* high-performance liquid chromatography.

Hpo *symbol for* the heptanoyl group, CH_3–$[CH_2]_5$–CO–.

HpODE *abbr. for* hydroperoxyoctadecadienoate.

HPR *abbr. for* H protein; a low-M_r, heat-stable, cytoplasmic phosphocarrier protein found in some bacterial species and concerned in the phospho*enol*pyruvate (PEP)-hexose transferase system for the transport of hexoses across the cell membrane. The phosphate of PEP is transferred transiently to HPR. Example from *Escherichia coli* (identical sequence for *Salmonella typhimurium*): database code PTHP_ECOLI, 85 amino acids (9.11 kDa). *See* **enzyme I**, **enzyme II**.

H^+ pump *see* **hydrogen ion pump**.

HQNO *see* **HOQNO**.

hr *abbr. for* hour (now superseded by h).

H1, H2, H3 receptors *see* **histamine receptor**.

H-RNA *abbr. for* heterogeneous nuclear RNA (alternative to hnRNA or HnRNA).

HRT *abbr. for* hybrid-released translation.

HSA *abbr. for* human serum albumin.

Hse *symbol for* a residue of the α-amino acid L-homoserine.

HSE *abbr. for* heat-shock regulatory element or heat-shock response element.

α_2-HS-glycoprotein *or* **fetuin** an α-globulin found in fetal calf serum, where it accounts for up to 45% of the total protein. It has a low isoelectric point and contains up to 35% carbohydrate, having three oligosaccharide chains each of M_r 3400; it comprises various glycoproteins that differ in M_r. It is a growth factor for a variety of cell types. It also promotes endocytosis, possesses opsonic properties, and influences the mineral phase of bone. The amino-acid sequence has **cystatin** features; two peptides are cleaved from a precursor to form chains held together by a single disulfide bond. Example precursor (human): database code A2HS_HUMAN, 367 amino acids (39.28 kDa).

Hsl *symbol for* a residue of the α-amino lactone L-homoserine lactone.

HSPG core protein *abbr. for* heparan sulfate proteoglycan core protein. *See also* **syndecan**.

hst/KS *see* ***KS/hst***.

H strand *abbr. for* heavy strand.

5-HT *abbr. for* 5-hydroxytryptamine (i.e. **serotonin**).

HTH *abbr. for* helix-turn-helix.

HTLV *abbr. for* human T-cell lymphotropic virus; a **retrovirus** that causes a rare leukemia.

H^+-transporting ATP synthase EC 3.6.1.34; *systematic name*: ATP phosphohydrolase (H^+-transporting); *other names*: H^+-transporting ATPase; mitochondrial ATPase; chloroplast ATPase; coupling factors $F_0{\cdot}F_1$, $C_0{\cdot}F_1$. The enzyme that is responsible for the phosphorylation of ADP to ATP in mitochondria, during **oxidative phosphorylation**. In *in vitro* preparations it can function as an ATPase. The 3-D structure is known for the major components of bovine heart mitochondrial enzyme (the following examples refer to this enzyme). The enzyme comprises an intrinsic membrane domain, F_0, linked by a stalk to a globular catalytic domain, F_1, and hence *is sometimes termed* F_0F_1 *complex*. Energy released by hydron flux through F_0 leads to ATP synthesis by F_1; the stoichiometry is approximately $3H^+$ per ADP phosphorylated. F_1 (371 kDa) has the subunit composition: $3\alpha,3\beta,\gamma,\delta,\varepsilon$; the subunit sequences (precursors) are: α, database code ATP0_BOVIN, 553 amino acids (59.65 kDa); β, database code ATPB_BOVIN, 528 amino acids (56.22 kDa); γ, database code ATPG_BOVIN, 297 amino acids (32.92 kDa); δ, database code ATPD_BOVIN, 168 amino acids (17.59 kDa); ε (from rat), database code ATPE_RAT, 50 amino acids (5.63 kDa). The γ chain forms a core, the α and β (catalytic) subunits are arranged round it alternately; the three β subunits have different structures during the synthesis cycle. The N- and C-terminal regions of γ form an antiparallel coiled coil; the α and β proteins are essentially β barrels. There are several proteins in the F_0 component, the main subunits of which in eukaryotes are named A to G. The C chain is the protein that accumulates in ceroid lipofuscinosis (**Batten's disease**). It is a proteolipid encoded by two genes which code for two precursor proteins, P_1 and P_2, having different signal peptides for locating the proteins in mitochondria, but the same structure in the mature protein. Example, subunit C precursor P_1 (bovine): database code ATPM_BOVIN, 143 amino acids (15.01 kDa). Other proteins of F_0 include the A chain, database code ATP6_BOVIN, 226 amino acids (24.8 kDa); the B chain, database code ATPF_BOVIN, 214 amino acids (24.64 kDa); and the D chain, database code ATPQ_BOVIN, 160 amino acids (18.56 kDa). (The last named chain has no apparent homologue in bacteria.)

huangosome *a colloquial term for* a bilayered **liposome**. *Compare* **bangasome**.

Huber, Robert (1937–), German biochemist notable for his crystallographic, immunological, and structural studies of proteins; Nobel Laureate in Chemistry (1988) jointly with J. Deisenhofer and H. Michel 'for the determination of the three-dimensional structure of a photosynthetic reaction centre'.

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Hudson's convention a convention, no longer used, for designating anomeric configurations in monosaccharides. The anomer in the D-series with the highest positive rotation (or lowest negative rotation) was designated the α form and the anomer with the lowest positive rotation was called the β form. The reverse applied in the L-series, the anomer with the lowest positive rotation (or the highest negative rotation) being designated the α form. The α and β descriptors now refer to the absolute structural relationships. *See* **anomer**, **Haworth representation**.

Hughes press a device to disrupt microorganisms. It consists of a steel cylinder in which a paste of the microorganisms in question, mixed with abrasives, is subjected to sudden blows by a steel piston driven by a fly-press; the piston forces the crushed material out of the cylinder into a reservoir. At temperatures below –20 °C no abrasives are needed, ice crystals taking their place. *See also* **French pressure cell**. [After D. E. Hughes (1922–), who published the design in 1951.]

HUGO *abbr. for* Human Genome Organization; an international organization of scientists involved in the **Human Genome Project**, the global initiative directed at mapping and sequencing the human genome. It was established in 1989, and carries out a coordinating role, supporting data collection for constructing genetic and physical maps of the human genome, organizing the Single Chromosome Workshops and other workshops and promoting consideration of ethical, legal, social, and intellectual property issues. It fosters exchange of data and biomaterials. The Human Genome Project is, however, not under the central control or direction of any individual, group, or organizing committee, the work being done in many countries being coordinated by the scientists carrying out the work.

human *abbr. (in bionomenclature)*: h *or (formerly)* H; of, relating to, characteristic of, obtained from, or being a member of the species *Homo sapiens*. For names of substances or products beginning with the word human (e.g. human chorionadotropin, human serum albumin) see at the corresponding general entry.

Human Genome Project *see* **HUGO**

human immunodeficiency virus *see* **HIV**.

human T-cell lymphotropic virus *see* **HTLV**.

humectant **1** producing moisture. **2** any substance added to another substance or material to keep it moist.

humic acid any of the mixture of complex macromolecules having polymeric phenolic structures and extractable from soils and peat. It is produced by the oxidative degradation of lignin and has the ability to chelate metals, especially iron.

humidity cabinet *or* **humidity chamber** an enclosure in which the humidity is maintained at a constant, often high level. It is useful for keeping experimental samples or materials moist or at a predetermined moisture content.

humin the very dark-brown or black insoluble material that is produced when carbohydrate-containing proteins are subjected to acid hydrolysis.

humor *the US spelling of* **humour**.

humoral of, contained in, or involving the blood or other body fluid; consisting of, relating to, or involving some chemical agent or substance contained in a body fluid, especially the blood.

humoral immunity any specific immunity mediated by antibodies (i.e. **humoral antibodies**) present in blood plasma, lymph, and tissue fluids, and that may also become attached to cells.

humour *or (US)* **humor** *a former name for* any of the body fluids, e.g. blood, lymph.

humulin **1** human insulin made using cDNA technology. **2** the bitter aromatic principle of hops (lupulin).

humus the dark-brown or black complex mixture of colloidal organic material that results from the decomposition of plant and animal material in the soil. It is of great importance for plant growth.

hunchback a segmentation protein in insects. Similar to **ikaros**, it is a zinc-finger protein and is encoded by a **gap gene**. Example from *Drosophila melanogaster*: database code HUNB_DROME, 758 amino acids (83.02 kDa). *Compare* **Krüppel**.

Hunter syndrome *an alternative name for* mucopolysaccharidosis II. *See* **mucopolysaccharidosis**. [After Charles Hunter (1872–1955), British physician.]

Huntington's disease *or* **Huntington's chorea** an autosomal dominant genetic disease characterized by involuntary (choreic) movements and dementia over a 10–20 year course. It is inevitably fatal. Linking studies using a variety of RFLPs have localized the defective gene to a site on the short arm of chromosome 4. There is a selective loss of a group of neurons; the biochemical basis for their loss is unknown. The gene, which encodes a 3145-residue product, **huntingtin**, of unknown function, contains a polymorphic trinucleotide repeat of the codon for glutamine, CAG, within the coding sequence. Normals have 35–37 of these repeats. In no case has any individual with more than 41 repeats been found to be free of the disease. [After George Huntington (1850–1916), US physician.]

HU protein an abundant bacterial histone-like protein that has the ability to wrap and bend DNA *in vitro*, and is thought to play a role in chromosome DNA topology, probably by facilitating the action of gyrase. *See* **DNA topoisomerase** type II.

Hurler–Scheie compound syndrome *an alternative name for* **mucopolysaccharidosis I H/S**.

Hurler syndrome *an alternative name for* mucopolysaccharidosis I H; *see* **mucopolysaccharidosis**. [After Gertrude Hurler (1889–1965), Austrian physician.]

HUT *(in clinical chemistry) abbr. for* UDPglucose-hexose-1-phosphate uridylyl transferase (EC 2.7.7.12).

Huxley **1 (Sir) Andrew Fielding** (1917–), British physiologist renowned for his researches on the ionic basis of contraction of muscle and of impulse conduction by nerve; Nobel Laureate in Physiology or Medicine (1963) jointly with J. C. Eccles and A. L. Hodgkin 'for their discoveries concerning the ionic mechanisms involved in excitation and inhibition in the peripheral and central portions of the nerve cell membrane'. **2 Hugh Esmor Huxley** (1924–), British biophysicist noted for his study of the relation of ATP hydrolysis to the mechanics of muscle contraction.

HVA *abbr. for* homovanillic acid.

HVE *abbr. for* high-voltage electrophoresis.

Hvidt–Nielsen mechanism a proposed mechanism to account for the kinetics of hydrogen exchange between protein molecules in solution and solvent water molecules. It is considered that protein molecules exist in solution in more than one conformational state and that hydrogen atoms in the interior of the protein molecule in the most stable conformational state are inaccessible to exchange; these hydrogen atoms may become transiently externalized, and hence accessible to exchange, in one or more of the other conformational states. [After Aasa Hvidt and S. O. Nielsen.]

Hx *abbr. for* hepoxilin.

Hx^c *symbol for* the cyclohexyl group (alternative to cHx).

hyal+ *a variant form of* **hyalo+** (before a vowel).

hyaladherin *a name sometimes used for* proteins in the **extracellular matrix** that bind to **hyaluronate**.

hyaline clear, transparent; with no inclusions.

hyalo+ *or (before a vowel)* **hyal+** *comb. form* denoting glassy, transparent.

hyaluronan *an alternative name for* **hyaluronate**.

hyaluronate *or* **hyaluronan** the naturally occurring anionic form of hyaluronic acid; any member of a group of glycosaminoglycans, the repeat units of which consist of $\beta1\rightarrow4$-linked D-glucuronyl-($\beta1\rightarrow3$)-*N*-acetyl-D-glucosamine. Most preparations contain 1–2% by mass of protein, and have M_r values in the range 5×10^4 to 8×10^6 depending on source and methods of preparation and determination. Hyaluronates are widely distributed in many tissues, especially in the vitreous humour of the eye, synovial fluid, and umbilical cord. They

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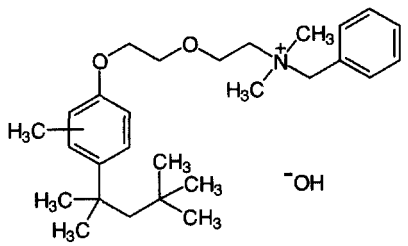
have an important role in the formation of proteoglycan aggregates. Hyaluronates form very viscous solutions and gels in water, a property that may be important in protecting animal organisms against invasion by bacteria.

hyaluronidase *or* **mucinase** *or* **spreading factor** *a trivial name for either of the glycosidases hyaluronoglucosaminidase* (EC 3.2.1.35) and hyaluronoglucuronidase (EC 3.2.1.36), and for the carbon–oxygen lyase hyaluronate lyase (EC 4.2.2.1). These enzymes have in common the ability to depolymerize hyaluronidate by cleavage of glycosidic bonds; e.g. hyaluronoglucosaminidase catalyses the random hydrolysis of 1,4-linkages between *N*-acetyl-*β*-D-glucosamine and D-glucuronate residues in hyaluronate. Hyaluronidases occur in certain animal tissues, e.g. sperm acrosome, and in some bacteria, e.g. *Clostridium* spp., and enhance the penetration of various substances and pathogens through the extracellular matrix (hence the name 'spreading factor'). Example, mu toxin from *Clostridium perfringens*: database code NAGH_CLOPE, 1042 amino acids (117.49 kDa).

hyamine hydroxide methylbenzethonium hydroxide; a water-soluble organic base, useful biochemically because it and some of its salts are soluble in organic solvents such as chloroform and toluene. It is therefore used to absorb radioactive CO_2 released during metabolic incubations; the resultant hyamine carbonate can then be dissolved in a scintillation cocktail for counting. It is also used as a topical anti-infective agent.



hybrid **1** something derived from heterogeneous sources or composed of different or incongruous elements. **2** *(in genetics)* the offspring of two animals or plants of different species, or (less strictly) different varieties. **3** *(in chemistry)* a bond or valence orbital obtained by the linear combination of two or more different atomic orbitals.

hybrid antibody any artificially produced immunoglobulin molecule in which the combining sites are of different specificities.

hybrid-arrested translation *abbr.*: HART; a method for analysing the relationship between a DNA sequence, its corresponding messenger RNA (mRNA), and the protein for which it codes, based on the observation that mRNA when hybridized with its complementary DNA is not translated in eukaryotic cell-free systems whereas heat-induced dissociation of the hybrid completely restores translational activity. The method has been used to map precisely specific protein-coding regions in **restriction fragments** of DNA. *See also* **hybrid-released translation**.

hybrid cell any cell containing the nuclei and cytoplasms from differing cells, formed artificially by **cell fusion**.

hybrid DNA **1** artificial duplex DNA produced by collinear (i.e. covalent) union of two (or more) fragments of duplex DNA (i.e. **recombinant DNA**; *see also* **plasmid chimera**). **2** artificial duplex DNA produced by collateral (hydrogen bonded) union of two incompletely complementary, single strands of DNA. *Compare* **DNA–RNA hybrid**.

hybridization *or* **hybridisation** **1** the act or process of forming a genetic **hybrid** (def. 2) by cross-breeding, or other unnatural recombination. **2** the act or process of forming a macromolecular **hybrid** (def. 1) by the artificial recombination of subunits, e.g. of polynucleotide strands or polypeptide chains. **3** the mathematical combination of atomic orbitals to form an orbital **hybrid** (def. 3).

hybridization analysis a method of testing for complementarity in the base sequences of two polynucleotides from different sources, based on the ability of complementary single-stranded DNA molecules to form duplex DNA molecules on being annealed together, and the ability of single strands of DNA and RNA similarly to form **DNA–RNA hybrids**.

hybridization probe *see* **probe** (def. 3).

hybrid myeloma *see* **hybridoma**.

hybridoma any permanent **cell line** derived from an artificial **somatic cell hybrid** formed between a cultured neoplastic lymphocyte and a normal primed B or T lymphocyte, all the cells of which express the specific immune potential of the normal parental cell. The term is derived from a contraction of 'hybrid' and 'myeloma'. Hybridomas are produced by the technique of **cell fusion**, using, e.g., a suspension of mouse myeloma or thymoma cells from a selected established cell line to which is added a preparation of spleen cells (predominantly normal lymphocytes) from mice or other animals that have been immunized against a specified antigen. After cell fusion, selection is aided by the use of **HAT** medium, which kills $HGPRT^-$ myeloma cells, and lymphocytes that have not fused do not survive in culture. This treatment thus selects for the immortalized hybridoma cells that retain the lymphocyte HGPRT. Such hybrid cells are both permanently adapted to growth in culture and capable of forming specific antibody-producing tumours *in vivo*. A B-cell hybridoma continuously secretes pure **monoclonal antibody** of a predetermined specificity and may thus be used for the facile large-scale production of such antibody.

hybrid-released translation *abbr.*: HRT; a method in which cloned DNA is bound to a nitrocellulose filter and hybridized with unfractionated mRNA, or even total cellular RNA. After washing the filter, any mRNA that has hybridized with the DNA is eluted and translated in a cell-free translation system, thus revealing the product that is encoded by the DNA. *See also* **hybrid-arrested translation**.

hydantoin *generic name for* 2,4-imidazolidinedione or its derivatives. A hydantoin is formed by the reaction of an isocyanate, commonly phenylisocyanate, with the free amino group of an amino acid and the cyclization of the hydantoic acid derivative initially formed. When an isocyanate reacts with the N-terminal amino group of a peptide, the corresponding hydantoin is formed with simultaneous cleavage of the substituted N-terminal amino-acid residue from the peptide.

hydr+ *a variant form of* **hydro+** (sometimes before a vowel).

hydrase *an obsolete term for* **hydratase**.

hydratase *see* **dehydratase**.

hydrate **1** any adduct of water with another compound or element, usually in definite molecular proportions. **2** to form a **hydrate** (def. 1); to undergo **hydration**. **3** to cause to take up or to combine with water. **4** to maintain or restore the normal proportion of water in the body (of someone or something). —**hydrated** *adj.*

hydration **1** the act or process by which water molecules surround and bind to molecular entities. **2** the addition of H and OH to a chemical species. **3** the formation of a **hydrate** (def. 1). **4** the quality or state of being hydrated. **5** the introduction of additional water into the body (of something or someone). *Compare* **anhydrous**, **dehydration**, **solvation**.

hydration shell the layer of water molecules surrounding an ion or molecule in aqueous solution.

hydraulic **1** operated by pressure transmitted through a liquid, e.g. through water or oil. **2** of or concerning hydraulics (i.e. fluid mechanics).

hydrazine $H_2N–NH_2$; an oily liquid, fuming in air, that is very toxic and possibly a carcinogen. It is available as a hydrate and as various salts. *See also* **hydrazinolysis**.

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hydrazinolysis the cleavage of amide and peptide bonds by heating at 100 °C with **hydrazine** in anhydrous conditions to form the corresponding acyl hydrazides. This reaction is useful in the determination of C-terminal amino-acid residues in peptides and proteins as all the other amino-acid residues will be converted to their hydrazides and only the C-terminal amino acid will be set free in an underivatized form.

hydrazone any condensation product of the type R′R″C=N–NHR, formed between carbonyl compounds (R′R″=CO) and hydrazine or a substituted hydrazine. *See also* **osazone**, **phenylhydrazone**.

hydride **1** the ion H^-, hydrogen anion. It has an independent existence only in the salt-like hydrides formed by strongly electropositive elements (*see* def. 2) but is also sometimes regarded as participating in the formation of complex hydrides (*see* def. 4) and in certain oxidation–reduction reactions (*see* **hydride-ion transfer**). **2** any stoichiometric binary compound of hydrogen with one of many (but not all) of the elements in groups 1, 2, and 3 of the IUPAC **periodic table**, e.g. NaH or CaH_2. Such hydrides are salt-like ionic compounds, are solids at ambient temperatures, and on fusion can be electrolysed (dihydrogen then being liberated at the anode). They are readily decomposed by water and are potent reducing agents. **3** Any stoichiometric compound of hydrogen with one (or sometimes more than one) of many of the elements in other groups of the periodic table, and also with boron. Such hydrides are volatile covalent compounds containing one atom of the element per molecule, e.g. PbH_4, or sometimes more than one, e.g. Si_3H_8; in the latter type certain of the hydrogen atoms may be present as bridges, as in B_2H_6. **4** any salt-like compound containing a complex anion that may be considered as formed by coordination of a hydride ion to an uncharged hydride, e.g. KBH_4 (*see* **borohydride**) or $LiAlH_4$; such compounds are widely used in organic chemistry as reducing agents or for introduction of tritium, ^3H. **5** any (frequently nonstoichiometric) product formed by uptake of dihydrogen by certain transition metals, especially palladium.

hydride-ion transfer *term conventionally often applied to* a chemical or enzyme-catalysed oxidation–reduction reaction involving the transfer from one molecule to another of a hydrogen atom together with its associated pair of bonding electrons. Such a reaction may notionally be considered to involve the transfer of a hydride ion without such an ion ever existing as a free entity. Examples include the **Cannizzaro reaction** and reactions of the general type

$$NADH + M + H^+ \rightleftharpoons NAD^+ + MH_2,$$

where M is a substrate molecule undergoing enzymic reduction, to which a hydride ion is transferred from NADH.

hydrindantin the reduced form of **ninhydrin**. It is sometimes used in conjunction with ninhydrin in the chromogenic determination or visualization of amino or imino groups.

hydrion *a former name for* **hydrogen ion**.

hydro+ *or (sometimes before a vowel)* **hydr+** *comb. form* **1** indicating or denoting water, liquid, or fluid. **2** indicating the presence of hydrogen in a compound.

hydrocarbon **1** any organic compound composed exclusively of hydrogen and carbon. **2** of, pertaining to, or being a **hydrocarbon** (def. 1) or a chemical group or side chain composed of hydrogen and carbon only.

hydrocarbyl any univalent group formed from a hydrocarbon by removal of a hydrogen atom; e.g. methyl (from methane).

hydrocolloid any colloidal substance for which the dispersing liquid is water or an aqueous solution.

hydrocortisone *an alternative name for* **cortisol**.

hydrodynamic **1** of or concerned with the mechanical properties of fluids. **2** of, pertaining to, or concerned with **hydrodynamics**.

hydrodynamic particle the entity formed by any (macro)molecule in solution together with its solvation shell.

hydrodynamic radius the radius of a (macro)molecule or other particle in solution as determined by a hydrodynamic method, e.g. sedimentation equilibrium.

hydrodynamics the branch of physics concerned with the forces acting on or exerted by fluids.

hydrodynamic shear the microscopic shear force caused by the motion of different layers in a fluid, where the layers move at different velocities. This acts to break any molecule sufficiently long to bridge the layers, e.g. DNA.

hydrodynamic volume *(of a molecule in solution)* the sum of the time-average of the molecular volume and the volume of the solvent molecules associated with it.

hydrogel any **gel** (def. 1) in which water is the liquid component. *Compare* **hydrosol**.

hydrogen *symbol*: H; the lightest of the elements and the most abundant in the universe. It exists as an odourless, colourless, flammable diatomic gas, dihydrogen, H_2, and forms compounds with most of the elements, being present in water and all organic compounds. There are two naturally occurring isotopes, hydrogen-1 (**protium**) and hydrogen-2 (**deuterium**), and one artificial isotope, hydrogen-3 (**tritium**), which is radioactive.

hydrogenase **1** *the recommended name for* an enzyme, EC 1.18.99.1, *also known as* **hydrogenlyase**, that catalyses the reaction:

$$2\ \text{ferredoxin}_{red} + 2H^+ = 2\ \text{ferredoxin}_{ox} + H_2.$$

This enzyme recycles H_2 produced by **nitrogenase** to increase the production of ATP and to protect nitrogenase against inhibition or damage by O_2. It is a heterodimer. Example from *Azotobacter vinelandii*: small subunit (precursor): database code MBHS_AZOVI, 358 amino acids (39.21 kDa); large subunit: database code MBHL_AZOVI, 602 amino acids (66.66 kDa). **2** *an alternative name for* **hydrogen dehydrogenase**. **3** EC 1.12.2.1; *recommended name*: cytochrome c_3 hydrogenase; an enzyme that catalyses the reaction:

$$H_2 + 2\ \text{ferricytochrome } c_3 = 2H^+ + 2\ \text{ferrocytochrome } c_3.$$

hydrogenate to undergo or cause to undergo reduction by addition of the hydrogen atoms of dihydrogen, usually with the aid of a catalyst such as finely divided forms of nickel, palladium, or platinum. The process is of industrial importance in petroleum refining, the petrochemical industry and the hardening of fats. —**hydrogenated** *adj.*; **hydrogenation** *n.*

hydrogen bond an association between an electronegative atom, e.g. fluorine, oxygen, nitrogen, or sulfur, and a hydrogen atom attached to another such electronegative atom. Although **hydrogen bonding** is due to interaction between dipoles, the force of attraction is large enough to permit formation of aggregates of small molecules or to stabilize the conformation of many macromolecules. The spatial relation of the donor and acceptor atoms is such that the hydrogen atom lies very close to the straight line between them.

hydrogen carrier *a name sometimes used for* any electron carrier that undergoes oxidation–reduction reactions by the loss or gain of hydrogen atoms, e.g. NADH, FADH.

hydrogen dehydrogenase *the recommended name for* the enzyme, EC 1.12.1.2, *also known as* **hydrogenase**, that catalyses the reaction:

$$H_2 + NAD^+ = H^+ + NADH.$$

It is a flavoprotein; iron and nickel are cofactors; the molecule is heterotetrameric. It may form part of a system involving **hydrogenase** (def. 1). Examples from *Alcaligenes eutrophus*: α subunit, database code HOXF_ALCEU, 602 amino acids (66.71 kDa); γ subunit, database code HOXU_ALCEU, 233 amino acids (26.01 kDa); the α and γ subunits form one dimer (FMN, 4Fe–4S cluster, NADH oxidoreductase); β subunit (contains Ni), database code HOXH_ALCEU, 487 amino acids (54.69 kDa); δ subunit, database code HOXY_ALCEU, 209 amino acids (22.85 kDa); the β and δ subunits form the other dimer which exhibits **hydrogenase** activity with artificial electron acceptors.

hydrogen–deuterium exchange *see* **hydrogen exchange**.

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hydrogen electrode an electrode that is reversible to hydrogen ions and dihydrogen molecules. It is formed by bubbling pure dihydrogen gas over a metal wire or a piece of foil whose surface is able to catalyse the reaction:

$$0.5H_2(g) = H^+ + e \qquad (1)$$

where e represents an electron. The most useful catalyst is platinum black on a platinum substrate. Hence the catalyst establishes an equilibrium between dihydrogen molecules (or hydrogen atoms) and the hydrogen ions (i.e. hydrons) in the solution in which the metal electrode is immersed. If the partial pressure (in atm) of dihydrogen gas at the electrode is p_{H_2}, the half-cell potential, E_H, of reaction (1) is given by:

$$E_H = E^\circ_H - (RT/F)\ln(a_{H^+}/p_{H_2}) \qquad (2)$$

where R is the gas constant, F the Faraday constant, T the thermodynamic temperature, and a_{H^+} the hydrogen-ion activity. E°_H, the standard potential of the hydrogen electrode, is, by convention, zero at all temperatures, hence at $p_{H_2} = 1$, the usual standard state, equation (2) becomes:

$$E_H = -(RT/F)\ln a_{H^+}.$$

Thus the hydrogen electrode is the ultimate reference electrode for the determination of pH values. It should be noted that the potential of any single electrode cannot be determined by itself; another electrode must be connected to the solution.

hydrogen exchange *or* **hydrogen–deuterium exchange** a technique useful for demonstrating conformational differences between samples of the same protein and for providing insight into the dynamics of protein conformations in solution. It can be observed using nuclear magnetic resonance spectroscopy. The method is based on observation of the kinetics of the non-catalysed exchange of hydrogen atoms in peptides and proteins with protons or other hydron isotopes in aqueous solutions and the effects of pH (or p^2H), temperature, etc. on the process.

hydrogen ion *or (formerly)* **hydrion** the cation, H^+, derived from the hydrogen atom. In aqueous solution it is mostly in the hydrated form, oxonium (H_3O^+). In nonaqueous solution it is likely, by analogy, that it is attached particularly to one solvent molecule, e.g. ROH_2^+ in an alcohol, R_2COH^+ in a ketone, RNH_3^+ in an amine, etc. *See also* **hydron**, **proton** (defs 1, 2).

hydrogen-ion concentration *see* **pH**.

hydrogen-ion pump any of a number of membrane proteins that transport hydrogen ions through membranes. The H^+-transporting ATPase of fungi and plants (EC 3.6.1.35) has an action similar to that of the **H^+-transporting ATP synthase** of mitochondria but without coupling factors; it is an integral membrane glycoprotein. The hydron gradient it generates drives the active transport of nutrients by H^+-symport. Example from yeast: database code ATH1_YEAST, 918 amino acids (99.42 kDa). The **vaculoar ATPase** is another type.

hydrogenlyase *see* **hydrogenase** (def. 1).

hydrogen lamp *or* **hydrogen discharge lamp** a high-voltage discharge tube with a quartz window and containing dihydrogen at low pressure, in which the glow produced by excitation of the dihydrogen molecules is concentrated in a long capillary tube joining the two electrodes; this arrangement gives increased intensity. It produces a continuous emission spectrum over the range 180–350 nm. *See also* **deuterium (discharge) lamp**.

hydrogenosome any microbody-like particle occurring in the cytoplasm of some anaerobic flagellate protozoans. They are chromatic granules of high density containing enzymes, including hydrogenase, that catalyse the conversion of pyruvate to acetate, CO_2, and H_2. These organelles may substitute for mitochondria (which are absent from such organisms).

hydrolase any enzyme of class EC 3 that catalyses the hydrolysis of various bonds, e.g. C–O, C–N, C–C, phosphoric anhydride bonds, etc. Often the name of a hydrolase is formed from the name of the substrate and the suffix '-ase'.

hydrolysate *or (sometimes US)* **hydrolyzate** any substance or mixture of substances produced by hydrolysis.

hydrolyse *or (sometimes US)* **hydrolyze** to subject to, to undergo, or to effect **hydrolysis**. —**hydrolysable** *or (US)* **hydrolyzable** *adj.*; **hydrolysation** *or (US)* **hydrolyzation** *n.*

hydrolysis (*pl.* **hydrolyses**) the rupture of one or more chemical bonds by reaction with, and involving the addition of, the elements of water; **solvolysis** by water.

hydrolytic of, pertaining to, producing, or produced by **hydrolysis**.

hydrolyzate *an alternative US spelling of* **hydrolysate**.

hydrolyze *an alternative US spelling of* **hydrolyse**.

hydrometer an instrument used to measure the **density**, or **relative density**, of a liquid. It usually consists of a glass (or plastic) bulb, weighted at the bottom so that it floats upright, and fitted with a stem carrying a scale. The point on the scale that is level with the surface of the liquid indicates the (relative) density of the liquid.

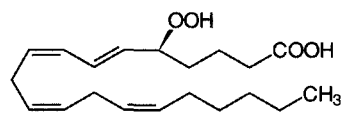
hydron *symbol*: H^+; *the recommended name for* the cation devised from an atom of hydrogen in its natural isotopic abundance. *See also* **hydrogen ion**, **proton** (defs 1, 2).

hydronate to combine with a **hydron** or hydrons. —**hydronation** *n.*

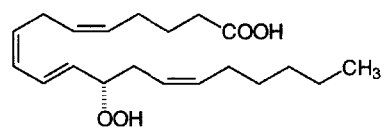
hydronium ion *an alternative name (now disfavoured) for* **oxonium** (def. 1).

hydroperoxide any organic compound in which one hydrogen atom of a hydrocarbon is replaced by the –O–OH group.

hydroperoxyeicosatetraenoate *abbr.*: HpETE; any of various related products of the action of **lipoxygenase** on arachidonate, (all-*Z*)-eicosa-5,8,11,14-tetraenoate. The most notable are 5(*S*)-HpETE, (6*E*,8*Z*,11*Z*,14*Z*)-(5*S*)-5-hydroperoxyeicosa-6,8,11,14-tetraenoate; 12(*S*)-HpETE, (5*Z*,8*Z*,10*E*,14*Z*)-(12*S*)-12-hydroperoxyeicosa-5,8,10,14-tetraenoate; and 15(*S*)-HpETE, (5*Z*,8*Z*,11*Z*,13*E*)-(*S*)-15-hydroperoxy-5,8,11,13-eicosatetraenoate. Their species distribution follows that of the lipoxygenases. HpETEs function as precursors of hydroxyeicosatetraenoates, leukotrienes, dihydroxyeicosatetraenoates, hepoxilins, and lipoxins, but they also have biological activity in their own right, e.g. regulation of electrolyte flux, release of histamine, regulation of eicosanoid and corticosterone synthesis, and regulation of oocyte maturation. 12-HpETE inhibits platelet thromboxane synthase and prostaglandin-endoperoxide synthase, and acts as a second messenger in *Aplysia* sensory neurons.



5(*S*)-HpETE



12(*S*)-HpETE

hydroperoxyoctadecadienoate *abbr.*: HpODE; any of various related products of the action of **lipoxygenase** on linoleate, (all-*Z*)-octadeca-9,12-dienoate. The most notable are 9(*S*)-HpODE, (10*E*,12*Z*)-(9*S*)-octadeca-10,12-dienoate; and 13(*S*)-HpODE, (9*Z*,11*E*)-(13*S*)-octadeca-9,11-dienoate.

hydrophilic **1** tending to dissolve in water; having a strong affinity for water; readily mixing with or wetted by water. *See also* **lyophilic**. **2 polar**. *Compare* **hydrophobic**. —**hydrophilicity** *n.*

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hydrophobic 1 tending not to dissolve in water; having a low affinity for water; not readily mixing with or wetted by water. 2 **nonpolar**. *Compare* **hydrophilic**. *See also* **lyophobic**. —**hydrophobicity** *n*.

hydrophobic bond *a term sometimes used incorrectly for* a **hydrophobic interaction**.

hydrophobic chromatography *or* **hydrophobic affinity chromatography** *or* **hydrophobic interaction chromatography** a technique for the separation and purification of proteins and other substances by **adsorption chromatography** on polysaccharide or other gels containing lipophilic substituents (which may or may not bear terminal ionizable groups). These hydrophobic centres on the gel interact with nonpolar amino-acid residues exposed on the surface of the protein molecules being separated.

hydrophobic interaction *or (discouraged)* **apolar bond** the tendency of hydrocarbons (or of lipophilic hydrocarbon-like groups in solutes) to form intermolecular or intramolecular aggregates in polar solvents. *See also* **apolar interaction**.

hydrophobic pocket *(in a protein)* a binding site (crevice, pocket) that contains mostly hydrophobic amino acids. For example, the binding site for the aromatic side chains of the specific substrates in **chymotrypsin** is a hydrophobic pocket, consisting of a slit in the enzyme, 100–120 nm deep and 35–40 nm by 55–65 nm in cross section, lined with nonpolar amino-acid side chains.

hydrophobic residue any building block of a polymer, the residue of which in that polymer is hydrophobic. The term is applied especially to amino-acid residues exhibiting such properties in polypeptides.

hydroquinone 1 1,4-benzenediol; *p*-dihydroxybenzene; quinol. *Compare* ***p*-benzoquinone**, **pyrocatechol**. *See also* **quinhydrone**. 2 any member of a class of aromatic *p*-diols derivable from *p*-quinones (*see* **quinone** (def. 2)) by reduction of two CO groups to COH groups with any necessary rearrangement of double bonds; any compound containing a quinol nucleus. *See also* **quinol** (def. 2), **semiquinone**. *Compare* **catechol** (def. 2).

hydrosol any **sol** in which water is the liquid component. *Compare* **hydrogel**.

hydrous *(of a chemical compound)* containing combined water (usually in stoichiometric proportions).

hydroxide 1 *or (formerly)* **hydroxyl** the ion OH^-. 2 any inorganic or organic compound containing or dissociating to give this ion. Hydroxides that are soluble in water, and can dissociate, give aqueous solutions with an alkaline reaction (pH > 7).

hydroxo+ *comb. form* indicating the presence of a OH^- ligand in a coordination compound.

hydroxocobalamin *or* **vitamin B_{12b}** a form of vitamin B_{12} in which a hydroxide ion is in coordinate linkage to the sixth (i.e. β) position on the cobalt atom in a molecule of **cobalamin**; the conjugate base of aquacobalamin.

hydroxonium ion *an alternative name (now disfavoured) for* **oxonium** (def. 1).

hydroxy denoting the presence in a compound of one or more **hydroxyl** groups.

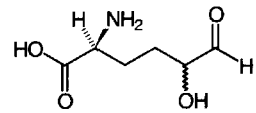
hydroxy+ *comb. form (in chemical nomenclature)* denoting the presence of one or more **hydroxyl** groups; the number of hydroxyl groups may be specified, e.g. dihydroxy+ (two), trihydroxy+ (three), etc.

hydroxy acid any organic acid containing one or more **hydroxyl** groups.

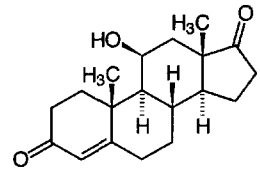
2-hydroxy-acid oxidase EC 1.1.3.15; *systematic name*: (*S*)-2-hydroxy-acid:oxygen 2-oxidoreductase; *other name*: glycolate oxidase; an enzyme that catalyses the oxidation by dioxygen of (*S*)-2-hydroxy-acid to 2-oxo-acid and H_2O_2. It is a peroxisomal enzyme in plants that is involved in the conversion of glycolate to glycine in **photorespiration**. The coenzyme is FMN. Example from *Spinacia oleracea*: database code GOX_SPIOL, 369 amino acids (40.28 kDa).

3-hydroxyacyl-CoA dehydrogenase EC 1.1.1.35; *systematic name*: (*S*)-3-hydroxyacyl-CoA:NAD^+ oxidoreductase; *other names*: β-hydroxyacyl dehydrogenase; β-keto-reductase; an enzyme of the **beta-oxidation system**. It catalyses the oxidation by NAD^+ of *S*-3-hydroxyacyl-CoA to 3-oxoacyl-CoA with formation of NADH; example (rat liver): database code RATD2D3COA, 287 amino acids (31.88 kDa); for another example (*Escherichia coli*): *see* **fatty-acid oxidation complex**. *See also* **peroxisomal bifunctional enzyme**.

hydroxyallysine 5-hydroxy-6-oxonorleucine; 2-amino-5-hydroxyadipaldehyde. An α-amino acid not normally found in proteins but enzymically formed from 5-hydroxylysine *in situ* as an intermediate in the creation of covalent cross-links between adjacent polypeptide strands during the maturation of certain connective tissue proteins, e.g. collagen, elastin. *See also* **allysine**.

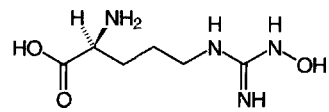


11β-hydroxy-4-androstene-3,17-dione 4-androsten-11β-ol-3,17-dione; a 17-oxo steroid formed from androstenedione by steroid 11β-monooxygenase (EC 1.14.15.4).



hydroxyapatite *or* **hydroxylapatite** a crystallized form of calcium orthophosphate hydroxide, $Ca_{10}(PO_4)_6(OH)_2$, virtually insoluble in water and in many aqueous solvents; it occurs as a mineral in phosphate rock. The main mineral component of bone, cartilage, and tooth approximates in composition to hydroxyapatite, small proportions of Ca^{2+} and OH^- being replaced respectively by Mg^{2+} and F^-; trace amounts of other ions may be present as well. Hydroxyapatite may also occur in granules in mitochondria. Chemically prepared hydroxyapatite is useful in the separation of proteins or nucleic acids by **adsorption chromatography**. It is used in orthopedic and dental prostheses and in the prevention of osteoporosis.

***N*$^{\omega}$-hydroxy-L-arginine** *abbr.*: L-NHA; a derivative of L-arginine in which one of the guanidine nitrogens is oxidized to an *N*-hydroxy group. It is an intermediate in the formation of nitric oxide from L-arginine; it may function as an intercellular NO carrier and a vasodilator in its own right.



***p*-hydroxybenzoic acid** 4-hydroxybenzoic acid; an intermediate in the synthesis of **ubiquinone** from tyrosine in mammals.

3-hydroxybutyrate cycle *or* **3-hydroxybutyrate shuttle** an intracellular metabolic cycle that can transfer reducing equivalents from the cytoplasm to the mitochondria in liver. Extramitochondrial NADH is oxidized to NAD^+ by acetoacetate, which is reduced to D(–)-3-hydroxybutyrate; the latter then passes into the mitochondria where it is reoxidized to acetoacetate by intramitochondrial NAD^+. The acetoacetate passes out into the cytoplasm thereby completing the cycle.

3-hydroxybutyrate dehydrogenase EC 1.1.1.30; *other*

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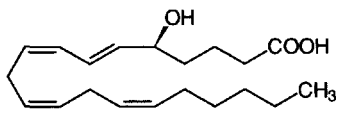
name: D-β-hydroxybutyrate dehydrogenase; an enzyme that catalyses the reaction:

(*R*)-3-hydroxybutanoate + NAD^+ = acetoacetate + NADH.

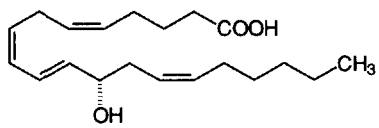
Example (fragment) from human: database code BDH_HUMAN, 343 amino acids (38.09 kDa).

α-hydroxybutyrate (2-hydroxybutanoate) dehydrogenase *an alternative name for* the LD_1 isoenzyme of **lactate dehydrogenase** (EC 1.1.1.27).

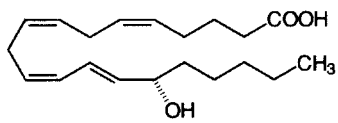
hydroxyeicosatetraenoate *abbr.*: HETE *or* mono-HETE; any of various related products arising, either spontaneously or by the action of glutathione peroxidases, from reduction of **hydroperoxyeicosatetraenoates**. The main forms are the 5-, 12-, and 15-HETEs, resulting from the action of 5-, 12-, and 15-**lipoxygenase** enzymes, but 8-, 9-, 11-, 16-, 17-, 18-, 19-, and 20-HETEs are known. The hydroxy group in most HETEs is of the *S* configuration, but those of *R* configuration are known, e.g. 12(*R*)-HETE from psoriatic lesions; 12(*R*)-HETE and 11(*R*)-HETE are found in sea-urchin eggs. The three main HETEs are: (6*E*,8*Z*,11*Z*,14*Z*)-(5*S*)-5-hydroxyeicosa-6,8,11,14-tetraen-1-oate, 5(*S*)-HETE; (5*Z*,8*Z*,10*E*,14*Z*)-(12*S*)-12-hydroxyeicosa-5,8,10,14-tetraen-1-oate, 12(*S*)-HETE; and (5*Z*,8*Z*,11*Z*,13*E*)-(15*S*)-15-hydroxyeicosa-5,8,11,13-tetraen-1-oate, 15(*S*)-HETE. Their tissue distribution follows that of **lipoxygenases**. 15(*S*)-HETE can act as a precursor for 5(*S*),15(*S*)-dihydroxyeicosatetraenoate and **lipoxins**. 5-HETE and 12-HETE are chemoattractants, 12(*R*) being more potent than 12(*S*), but 5(*S*) being more potent than 5(*R*); 8(*R*)-HETE, synthesized by starfish oocytes, is orders of magnitude more potent than 8(*S*)-HETE in inducing oocyte maturation.



5(*S*)-HETE



12(*S*)-HETE



15(*S*)-HETE

hydroxy fatty acid any member of a class of fatty acids having a hydroxyl group, usually at the 2- or 3-position. 2-D(–)-hydroxy fatty acids are widespread minor constituents of plant and some animal (wool, skin) lipids; 3-L(+)-hydroxy fatty acids are found in low amounts in plant and bacterial lipids (e.g. in **mycolic acids**). Mid-chain hydroxy acids and polyhydroxy acids also occur in plant lipids.

5-hydroxyindoleacetaldehyde *see* **5-hydroxyindole metabolism**.

5-hydroxyindoleacetic acid *abbr.*: 5-HIAA; a metabolite of **5-hydroxytryptamine**, produced by oxidative deamination catalysed by the enzyme **monoamine oxidase**, followed by oxidation to 5-HIAA. *See also* **5-hydroxyindole metabolism**.

5-hydroxyindole metabolism the metabolism of 5-hydroxytryptophan and its derivatives; it is of particular interest because it is concerned with the synthesis and degradation of the neurotransmitter 5-hydroxytryptamine (i.e. **serotonin**). Serotonin is converted to 5-hydroxy-3-indoleacetaldehyde by **monoamine oxidase**, and thence to either 5-hydroxytryptophol (3%) or 5-hydroxy-3-indoleacetic acid (5-HIAA) (97%), and these are excreted in the urine. Urinary 5-HIAA is measured as a diagnostic aid in cases of carcinoid syndrome, as the tumour converts large amounts of dietary tryptophan to serotonin.

hydroxyl **1** the (covalently linked) –OH group in any chemical compound. **2** *a former name for* the hydroxide ion; *see* **hydroxide** (def. 1).

hydroxylamine **1** NH_2–OH; a chemical mutagen that causes the deamination of cytosine residues in DNA so that, during subsequent replication of the DNA, the altered cytosine pairs with adenine rather than with guanine, causing G–C to A–T transitions. Hydroxylamine is an intermediate in the oxidation of ammonium in nitrifying bacteria, and in the reverse reaction in denitrifying bacteria. It may be used to cleave specifically Asp-|-Gly bonds in peptides. **2** any organic compound of the type RNH–OH.

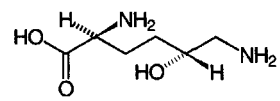
hydroxylapatite *an alternative name for* **hydroxyapatite**.

hydroxylase *the common name for* many monooxygenase and a few **dioxygenase** enzymes that catalyse hydroxylation reactions.

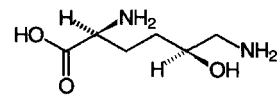
hydroxylate to introduce one or more **hydroxyl** (def. 1) groups into a compound, often by the replacement of hydrogen atom(s). —**hydroxylation** *n.*

hydroxylation-induced migration *an alternative name for* **NIH shift**.

hydroxylysine *the trivial name for* δ-hydroxylysine; δ-hydroxy-α,ε-diaminocaproic acid; 5-hydroxy-2,6-diaminohexanoic acid; H_2N–CH_2–CHOH–$[CH_2]_2$–$CH(NH_2)$–COOH; a chiral α-amino acid. Because the molecule of hydroxylysine possesses two chiral centres, four isomeric forms are possible, comprising an enantiomeric (D_s and L_s) pair of each of two (*erythro* and *threo*) diastereoisomers (the pair of *threo* enantiomers are sometimes known as **allohydroxylysine**). L-Hydroxylysine (*symbol*: 5Hyl *or* Hyl *or* Lys(5-OH) *or (formerly)* Hylys), *erythro*-5-hydroxy-L_s-lysine, is a **noncoded amino acid** found in peptide linkage in proteins (mainly collagen). In collagen 15–20% of the lysine residues are enzymically converted to hydroxylysine residues while the growing peptide chains are still attached to ribosomes; some of the hydroxyl groups of the hydroxylysine side chains are subsequently glycosylated.



L-hydroxylysine



L-allohydroxylysine

hydroxy-methoxymandelate *abbr.*: HMMA; 4-hydroxy-3-methoxymandelate; *often (incorrectly) known as* vanillylmandelate (*abbr.*: VMA); the L enantiomer is the end product of

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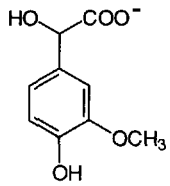
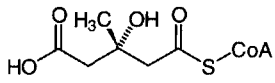
catecholamine catabolism, and is excreted in the urine. In clinical chemistry the measurement of HMMA in urine is used to detect excessive biosynthesis of catecholamines, as, e.g., in **pheochromocytoma**.



hydroxymethylbilane synthase EC 4.3.1.8; *systematic name*: porphobilinogen ammonia-lyase (polymerizing); *other names*: porphobilinogen deaminase; pre-uroporphyrinogen synthase. An enzyme that catalyses the conversion of four molecules of porphobilinogen to hydroxymethylbilane and four molecules of ammonia; dipyrromethane is a cofactor. Together with **uroporphyrinogen-III synthase** it is responsible for the step in heme biosynthesis in which four porphobilinogen molecules are condensed to form uroporphyrinogen III. Example from *Escherichia coli*: database code HEM3_ECOLI, 313 amino acids (33.81 kDa); 3-D structure known.

5-hydroxymethylcytosine *abbr.*: HMC; a minor base occurring in some types of DNA, e.g. in T4 bacteriophage.

hydroxymethylglutaryl-CoA *abbr.*: HMG-CoA; *β*-hydroxy-*β*-methylglutaryl-CoA; (*S*)-3-hydroxy-3-methylglutaryl-CoA; an important intermediate in the synthesis of cholesterol, farnesyl and geranyl derivatives, and ketone bodies. *See also* **hydroxymethylglutaryl-CoA reductase**, **hydroxymethylglutaryl-CoA lyase**.



hydroxymethylglutaryl-CoA lyase *abbr.*: HMG-CoA lyase; EC 4.1.3.4; *systematic name*: (*S*)-3-hydroxy-3-methylglutaryl-CoA acetoacetate lyase. An enzyme that catalyses the formation of acetyl-CoA and acetoacetate from (*S*)-3-hydroxy-3-methylglutaryl-CoA.
In mammals, a mitochondrial enzyme that converts hydroxymethylglutaryl-CoA to acetoacetate in the synthesis of **ketone bodies**. Example from *Pseudomonas mevalonii*: database code MVAB_PSEMV, 301 amino acids (31.57 kDa).

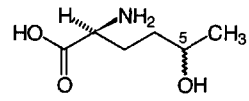
hydroxymethylglutaryl-CoA reductase (NADPH) *abbr.*: HMG-CoA reductase; EC 1.1.1.34; *systematic name*: (*R*)-mevalonate:NADP$^+$ oxidoreductase (CoA-acylating). An enzyme that catalyses a reaction between (*S*)-3-hydroxy-3-methylglutaryl-CoA and two molecules of NADPH to form (*R*)-mevalonate, CoA, and two molecules of NADP$^+$. Its function is to reduce HMG-CoA to (*R*)-mevalonate. In mammals it is an integral membrane glycoprotein of endoplasmic reticulum and peroxisomes. It catalyses a rate-limiting step and is an important regulatory enzyme in pathways for the synthesis of cholesterol and other sterols. It is the target for therapeutic strategies for reducing plasma cholesterol. Example from human: database code HMDH_HUMAN, 888 amino acids (97.36 kDa). *See also* **dephospho-[reductase kinase] kinase**.

[hydroxymethylglutaryl-CoA reductase (NADPH)] kinase EC 2.7.1.109; *other name*: reductase kinase; an enzyme that catalyses the phosphorylation by ATP of [3-hydroxy-3-methylglutaryl-CoA reductase (NADPH)] with release of ADP. It thereby inactivates the latter enzyme.

[hydroxymethylglutaryl-CoA reductase (NADPH)]-phosphatase EC 3.1.3.47; *other name*: reductase phosphatase; an enzyme that hydrolyses phosphate from [hydroxymethylglutaryl-CoA reductase (NADPH)] phosphate. It thereby activates the latter enzyme.

hydroxymethylglutaryl-CoA synthase *abbr.*: HMG-CoA synthase; EC 4.1.3.5; *systematic name*: (*S*)-3-hydroxy-3-methylglutaryl-CoA acetoacetyl-CoA-lyase (CoA-acetylating). An enzyme that catalyses a reaction between acetyl-CoA + H_2O and acetoacetyl-CoA to form (*S*)-3-hydroxy-3-methylglutaryl-CoA and CoA. In mammals it is a cytoplasmic and mitochondrial enzyme, catalysing the formation of hydroxymethylglutaryl-CoA from acetoacetyl-CoA and acetyl-CoA in cytoplasm for sterol biosynthesis, or in mitochondria for **ketone body** synthesis. Example from human: database code HMCS_HUMAN, 520 amino acids (57.29 kDa).

5-hydroxynorleucine *an older name (no longer recommended) for* 2-amino-5-hydroxyhexanoic acid; a nonprotein (non-coded) amino acid found in plants, e.g. *Crotolaria juncea*.



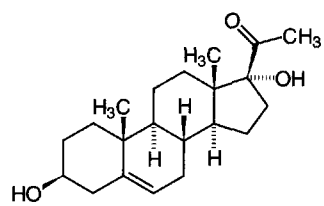
(*R*)-4-hydroxyphenyllactate dehydrogenase EC 1.1.1.222; *other name*: (*R*)-aromatic lactate dehydrogenase; an enzyme that catalyses the reaction:

(*R*)-3-(4-hydroxyphenyl)lactate + NAD(P)$^+$ =
3-(4-hydroxyphenyl)pyruvate + NAD(P)H.

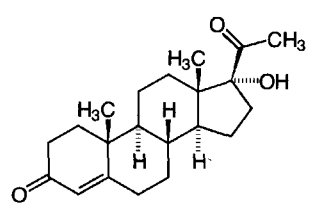
hydroxyphenylpyruvate reductase EC 1.1.1.237; an enzyme that catalyses the reaction:

3-(4-hydroxyphenyl)lactate + NAD$^+$ =
3-(4-hydroxyphenyl)pyruvate + NADH.

17*α*-hydroxypregnenolone 3*β*,17-dihydroxy-5-en-20-one; an intermediate in the synthesis of androgens, estrogens, and glucocorticoid hormones from cholesterol in the adrenal cortex. It is formed from **pregnenolone** by steroid 17*α*-monooxygenase (EC 1.14.99.9).



17*α*-hydroxyprogesterone 17-hydroxypregn-4-one; an intermediate in the synthesis of androgens, estrogens, and glucocorticoid hormones from cholesterol in the adrenal cortex. It is formed from **progesterone** by steroid 17*α*-monooxygenase (EC 1.14.99.9).



hydroxyproline *symbol*: Hyp *or (formerly)* Hypro; either of the two constitutional isomers 3-hydroxyproline and 4-hy-

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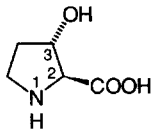
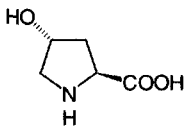
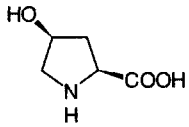
droxyproline, HO–(C_4H_6NH)–COOH, both of which are chiral cyclic N-alkylated α-amino acids. Each constitutional isomer possesses two chiral centres; each can therefore exist as an enantiomeric (D and L) pair of each of two (*cis* and *trans*) diastereoisomers, making eight possible isomeric structures for hydroxyproline in all. Both *trans*-3-hydroxy-L-proline (*symbol*: 3Hyp *or* Pro(3-OH)), (2*S*,3*S*)-3-hydroxypyrrolidine-2-carboxylic acid, and *trans*-4-hydroxy-L-proline (*symbol*: 4Hyp *or* Pro(4-OH)), (2*S*,4*R*)-4-hydroxypyrrolidine-2-carboxylic acid, are **noncoded amino acids** found in peptide linkage in proteins. In collagen nearly 50% of the proline residues are hydroxylated to 4Hyp and a small proportion to 3Hyp; hydroxyproline residues are also found in elastin, enamel of the teeth, in the C1a moiety of the C1 component of **complement**, and in **extensin**. In collagen formation, enzymic hydroxylation of proline residues occurs while the growing peptide chains are still attached to ribosomes. Residues of both the *cis*-(2*S*,3*R*)-, and the *trans*-(2*S*,3*S*)-isomers of 3-hydroxy-L-proline, one of each per molecule, occur in the peptide antibiotic telomycin. One residue per molecule of *cis*-4-hydroxy-L-proline, the (2*S*,4*S*)-isomer, occurs in every member of the **amatoxin** group of toxic fungal octapeptides. None of the D series of isomers is known to occur naturally.



trans-(2*S*,3*S*)-3-hydroxy-L-proline



trans-(2*S*,4*R*)-4-hydroxy-L-proline



cis-(2*S*,4*S*)-4-hydroxy-L-proline

hydroxyprolinemia *or* **hyperhydroxyprolinemia** a metabolic disorder of humans characterized by high levels of free 4-hydroxyproline in the blood plasma and urine. It is probably due to a deficiency in the activity of so-called hydroxyproline oxidase, i.e. the enzyme 4-oxoproline reductase (EC 1.1.1.104).

15-hydroxyprostaglandin dehydrogenase (NAD$^+$) EC 1.1.1.141; an enzyme involved in the inactivation of prostaglandins E_2, $F_{2\alpha}$, and B_1, by oxidizing the 15-hydroxyl group to a keto group. It catalyses a reaction between (5*Z*,13*E*)-(15*S*)-11α,15-dihydroxy-9-oxoprost-5,13-dienoate and NAD^+ to form (5*Z*,13*E*)-11α-hydroxy-9,15-dioxoprost-5,13-dienoate (15-keto PGE_2) and NADH. Example from human: database code PGDH_HUMAN, 266 amino acids (28.94 kDa).

5-hydroxytryptamine *abbr.*: 5-HT; *an alternative name for* **serotonin**.

5-hydroxytryptamine receptor any of several membrane proteins that bind 5-hydroxytryptamine (i.e. **serotonin**) and mediate its intracellular effects. The receptors are classified pharmacologically into seven main subtypes or families; the members of these are designated 5-HT_{1A}, 5-HT_{1B}, 5-HT_{1D}, 5-HT_{1E}, 5-HT_{1F}, 5-HT_{2A}, 5-HT_{2B}, 5-HT_{2C}, 5-HT_3, 5-HT_4, 5-HT_{5A}, 5-HT_{5B}, 5-HT_6, and 5-HT_7. The members of the 5-HT_1 family all have seven transmembrane domains and are negatively coupled to adenylate cyclase through G-proteins, but the 5-HT_{1A} receptor also increases K^+ conductance; example, 5-HT_{1A} from rat: database code 5HIA_RAT, 422 amino acids (46.43 kDa). 5-HT_{1C} is now classified as a 5-HT_2 receptor. 5-HT_{2A}, 5-HT_{2B}, and 5-HT_{2C} have seven transmembrane domains and activate the phosphatidylinositol cycle; example, 5-HT_{2C} from rat: database code 5H2C_RAT, 460 amino acids (51.92 kDa). 5-HT_3 opens a Cl channel; 5-HT_4 has four transmembrane domains and is positively coupled to adenylate cyclase; 5-HT_5 has seven transmembrane domains but the main effector is unknown; example, 5-HT_{5A} from rat: database code 5H5A_RAT, 357 amino acids (40.67 kDa). 5-HT_6 and 5-HT_7 are both of the seven-transmembrane-helix type and are positively coupled to adenylate cyclase.

5-hydroxytryptophan a nonprotein amino acid found in plants; it is formed in legumes by hydroxylation of tryptophan. It is also formed in animals. *See also* **serotonin**.

hydroxyurea $NH_2CONHOH$; an analogue of **urea** with antineoplastic activity, possibly through inhibition of DNA synthesis.

hygro+ *comb. form* denoting moisture, especially that due to water.

hygrometer any instrument for measuring the relative humidity of a gas.

hygromycin B an aminoglycoside antibiotic from *Streptomyces hygroscopicus*; the inclusion of genes conferring resistance to hygromycin B in certain fungal recombinant DNA vectors allows selection of recombinants when these are plated out on medium containing this antibiotic.

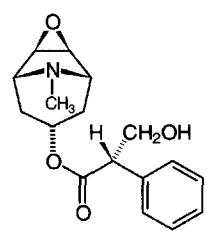
hygroscopic *(of a substance)* tending to absorb water from the surrounding atmosphere. *Compare* **deliquescent**.

Hyl *or (formerly)* **Hylys** *symbol for* a residue of any of the hydroxy derivatives of the α-amino acid L-lysine, especially 5-hydroxy-L-lysine. *See* **hydroxylysine**.

5Hyl *symbol for* a residue of the α-amino acid 5-hydroxy-L-lysine *(preferred alternative to* Lys(5-OH) or Hyl). *See* **hydroxylysine**.

Hylys *former symbol for* a residue of (5-)hydroxy-L-lysine (5Hyl or Hyl now recommended).

hyoscine *or* **scopolamine** an alkaloid found, e.g., in *Datura stramonium* (thorn apple) and related to **atropine** in its structure and effects; it is a tertiary ammonium compound noted for its actions as a **muscarinic receptor** antagonist. It has found use as a sedative and preanesthetic and for prevention of motion sickness.



hyoscyamine 3α-tropanyl S-(–)-tropate; an anticholinergic material obtained from *Atropa belladonna* and other plants. It undergoes partial racemization on isolation; this process is completed by alkali treatment, and the racemic mixture is known as atropine. (Illustrated on p. 318.)

hyp+ *a variant form of* **hypo+** *(before a vowel)*.

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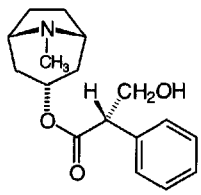

(–)-hyoscyamine

Hyp **1** *or (formerly)* **Hypro** *symbol for* a residue of either the 3-hydroxy or the 4-hydroxy derivative of the α-amino (strictly, α-imino) acid L-proline, usually 4-hydroxy-L-proline. *See* **hydroxyproline**. *See also* **3Hyp**, **4Hyp**. **2** *symbol for* a residue of the purine base **hypoxanthine**.

3Hyp *symbol for* a residue of the α-amino acid 3-hydroxy-L-proline (*preferred alternative to* Pro(3-OH) or Hyp). *See* **hydroxyproline**.

4Hyp *symbol for* a residue of the α-amino acid 4-hydroxy-L-proline (*preferred alternative to* Pro(4-OH) or Hyp). *See* **hydroxyproline**.

hypelcin A a 20-residue peptide of microbial origin containing 10 α-aminoisobutyric acid residues. The N terminus is acylated and the C terminus amidated with **leucinol**. It modifies the permeability of phospholipid bilayers.

hyper+ *prefix* indicating over, beyond, excessive, or in excess; above the normal range. *Compare* **hypo+**, **normo+**.

hyperaldosteronism an elevated level of **aldosterone** in the blood. In primary aldosteronism, there is overproduction of aldosterone due to a lesion of the adrenal(s), e.g. an adrenal tumour as in Conn's syndrome. In secondary aldosteronism the overproduction is caused by excessive levels of stimulatory hormones, especially increased renin secretion.

hyperammonemia *or (esp. Brit.)* **hyperammonaemia** the presence of excess ammonia in the blood (the normal range is 10–47 μmol L^{-1}). It occurs in a number of conditions including inherited disorders of the urea cycle, organic acidemias, liver disease, and severe systemic illness. *See also* **ornithine–urea cycle**.

hyperbaric of, relating to, or operating at higher than normal pressures.

hyperbilirubinemia *or (esp. Brit.)* **hyperbilirubinaemia** the presence of higher than normal concentrations of **bilirubin** in the blood; it may involve unconjugated or conjugated bilirubin. It occurs in liver disease or biliary obstruction, and is characteristic of neonatal hemolytic **jaundice**, where the bilirubin is mainly unconjugated. —**hyperbilirubinemic** *or* **hyperbilirubinaemic** *adj.*

hyperbola one of the conic sections; a plane curve in which the focal distance of any point bears to its distance from the directrix a constant ratio greater than unity. It has two foci and two asymptotes. *Compare* **rectangular hyperbola**. —**hyperbolic** *adj.*

hyperbolic function any one of a group of functions of an angle, analogous to the trigonometric functions, expressed as a relationship between the distances of a point on a hyperbola to the origin and to the coordinate axes. The group includes sinh (hyperbolic sine), defined as $\sinh x = (e^x - e^{-x})/2$; cosh (hyperbolic cosine), defined as $\cosh x = (e^x + e^{-x})/2$; and tanh (hyperbolic tangent), defined as $\tanh x = (\sinh x)/(\cosh x)$. The corresponding reciprocal functions are cosech (hyperbolic cosecant), sech (hyperbolic secant), and coth (hyperbolic cotangent), respectively.

hyperbolic kinetics curve *a description sometimes used of* the $v/[S]$ plot obtained for enzymes exhibiting **Michaelis–Menten kinetics**. The axes of the plot are not those of the rectangular hyperbola that results, but are rotated 45° (and displaced) from the true axes of the hyperbola.

hypercalcemia *or (esp. Brit.)* **hypercalcaemia** the presence of higher than normal concentrations of **calcium** in the blood. Clinical features include tiredness, muscle weakness, anorexia, weight loss, cardiac arrhythmia, and hypertension. It arises from a multiplicity of causes including malignancy, primary hyperparathyroidism, hyperthyroidism, acute adrenal insufficiency, familial hypocalciuric hypercalcemia, vitamin D or A overdose, or sarcoidosis. —**hypercalcemic** *or* **hypercalcaemic** *adj.*

hypercapnia *or* **hypercarbia** the presence of greater than normal amounts of carbon dioxide in a vertebrate or in its blood. *Compare* **hypocapnia**. —**hypercapnic** *or* **hypercarbic** *adj.*

hyperchlorhydria the presence of greater than normal amounts of hydrochloric acid in the gastric juice. **hyperchlorhydric** *adj.*

hypercholesterolemia *or (esp. Brit.)* **hypercholesterolaemia** the presence of higher than normal concentrations of cholesterol in the blood. *See also* **hyperlipidemia** —**hypercholesterolemic** *or* **hypercholesterolaemic** *adj.*

hyperchromatic **1** of, relating to, or exhibiting **hyperchromatism**. **2** *an alternative word for* **hyperchromic** (def. 1).

hyperchromatism the condition or property (of a cell or cell organelle) of staining more intensely than normal; the presence of a greater than normal amount of chromatin.

hyperchromic **1** *or* **hyperchromatic** more highly coloured than normal; intensely coloured. **2** of, pertaining to, exhibiting, or resulting from **hyperchromism**. **3** *(of a substance)* displaying a **hyperchromic effect**. **4** describing erythrocytes that contain, or appear to contain, more hemoglobin than normal.

hyperchromic effect the large increase in absorption of ultraviolet light, usually measured at 260 nm, shown by a solution of any natural or synthetic polynucleotide with a hydrogen-bonded structure when it is denatured or degraded. The effect is due to alterations in the electronic interactions between the initially stacked and hydrogen-bonded bases.

hyperchromicity a measure of the increase in absorption of electromagnetic radiation at a specific wavelength, usually that of the absorption maximum, due to **hyperchromism**, or to the **hyperchromic effect**. It is equal to the reciprocal of the **hypochromicity** minus unity.

hyperchromism the increased absorption of electromagnetic radiation exhibited by an ordered structure above that predicted on the basis of its constitution.

hyperfine splitting the splitting of a spectral line into multiplets of closely spaced lines. In electron spin resonance spectra hyperfine splitting is due to the interaction of unpaired electrons with neighbouring nuclei and can be used to determine the structure of a free radical or to identify the ligands of a paramagnetic ion and to measure the degree of covalent binding that exists between them. In nuclear magnetic resonance spectra hyperfine splitting, sometimes called **spin–spin splitting**, is due to the interaction of the nuclear magnetic moment with those of neighbouring nuclei and can be used to assign particular nuclear resonances and to determine molecular conformations.

hyperfine structure the presence in a spectrum of multiplets of closely spaced lines resulting from **hyperfine splitting**.

hyperglycemia *or (esp. Brit.)* **hyperglycaemia** an abnormally high blood glucose concentration, especially in relation to the fasting value. *See also* **glycemia**. —**hyperglycemic** *or* **hyperglycaemic** *adj.*

hyperglycemic factor *or* **hyperglycemic-glycogenolytic factor** *a former name for* **glucagon**.

hyperhydroxyprolinemia *see* **hydroxyprolinemia**.

hyperimmune describing the state of an animal in which very high concentrations of specific antibody are present in the serum, brought about by **hyperimmunization**.

hyperimmunization *or* **hyperimmunisation** any method of immunization designed to stimulate the production in the animal immunized of very large quantities of specific antibody. It typically involves the repeated administration of immunogen, often in increasing amounts.

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hyperkalemia *or (esp. Brit.)* **hyperkalaemia** the presence in the blood of an abnormally high concentration of **potassium**. There are many causes including excessive K^+ intake (infusion, transfusion), increased transcellular movement (tissue damage, systemic acidosis), and decreased K^+ loss (renal failure, mineralocorticoid deficiency). —**hyperkalemic** *or* **hyperkalaemic** *adj.*

hyperlactatemia *or (esp. Brit.)* **hyperlactataemia** a clinical condition characterized by a persistent raised blood lactate concentration, usually below 5 mmol L^{-1}, and not accompanied by a lowered blood pH. The normal range is between 0.5 and 2.2 mmol L^{-1}. *Compare* **lactic acidosis**. —**hyperlactatemic** *or* **hyperlactataemic** *adj.*

hyperlipidemia *or* **hyperlipemia** *or (esp. Brit.)* **hyperlipidaemia** *or* **hyperlipaemia** the presence in the blood of an abnormally high concentration of fats (or lipids). Hyperlipidemias have been classified into various types according to which lipoprotein class is found to be elevated in the blood. The Fredrickson classification scheme designates: type I, elevated chylomicrons; type II, elevated low-density lipoprotein; type III, elevated intermediate-density lipoprotein; type IV, elevated very-low-density lipoprotein; type V, elevated chylomicrons and very-low-density lipoprotein. A simpler distinction, of use in treatment, is between elevated cholesterol levels (type II, **hypercholesterolemia**) and elevated triacylglycerol levels (types I, III–V, **hypertriglyceridemia**, an older term still often used). Hyperlipidemia may be secondary to other conditions; several drugs cause or exacerbate hyperlipidemia, including thiazides, **beta blockers** lacking intrinsic sympathomimetic activity, and **corticosteroids**. Estrogens may lower hypercholesterolemia, but may cause or exacerbate hypertriglyceridemia; hypothyroidism is commonly associated with hypercholesterolemia; high alcohol intake causes hypertriglyceridemia, but modest alcohol intake may have a beneficial effect on cholesterol status, as it tends to increase **high-density lipoprotein** concentration. —**hyperlipidemic**, **hyperlipemic** *or* **hyperlipidaemic**, **hyperlipaemic** *adj.*

hypermodified base any extensively modified nucleic-acid base occurring adjacent to the 3′ end of the anticodon in many tRNA molecules. Examples are N^6-(δ_2-isopentenyl)adenosine (*symbol*: iA) and N^6-(threonylcarbamoyl)adenosine (*symbol*: tA). Hypermodified bases are thought to be important for proper binding of tRNA molecules to ribosomes.

hypernatremia *or (esp. Brit.)* **hypernatraemia** the presence in the blood of an abnormally high concentration of sodium. It may be associated with conditions in which body water is depleted. —**hypernatremic** *or* **hypernatraemic** *adj.*

hyperoxaluria the presence of oxalate in the urine in abnormally high amounts. Primary hyperoxaluria is a rare inherited metabolic disorder of which there are two types: one results in increased oxalate synthesis, the other in increased oxalate excretion by the kidney. More usually, hyperoxaluria results from increased absorption of oxalate from the intestine. It is associated with the formation of renal calculi.

hyperoxia the presence of greater than normal amounts of dioxygen in a vertebrate or in its blood. *Compare* **hypoxia**. —**hyperoxic** *adj.*

hyperparathyroidism the increased production of **parathyroid hormone**. It may be primary, as a result of a tumour of the parathyroid gland, or secondary, as a result of a disturbance in calcium metabolism.

hyperphosphatemia *or (esp. Brit.)* **hyperphosphataemia** an excessive level of phosphate in the blood. It occurs most commonly in renal insufficiency, but may also accompany hypoparathyroidism, vitamin D intoxication, or excessive administration of phosphate. —**hyperphosphatemic** *or* **hyperphosphataemic** *adj.*

hyperplasia the increase in size of a tissue or organ resulting from an increase in the total number of cells present. The part thus affected retains its normal form. *Compare* **hypertrophy**. —**hyperplastic** *adj.*

hyperprolactinemia *or (esp. Brit.)* **hyperprolactinaemia** the presence in the blood of abnormally high levels of **prolactin**, due to excessive secretion of the hormone. The most common example of pituitary hyperfunction, it results from pituitary adenoma, and also from treatment with dopamine receptor blockers. It can be treated with dopamine agonists, e.g. **bromocriptine**. —**hyperprolactinemic** *or* **hyperprolactinaemic** *adj.*

hypersecretion excessive secretion by any endocrine or exocrine gland.

hypersensitive having an abnormally great sensitivity, especially to an allergen, drug, or other agonist.

hypersensitivity **1** the state or condition of being **hypersensitive**. **2** *(in immunology)* an immune response that occurs in an exaggerated or inappropriate form. Such responses may result from agents including pollen or drugs, or from genuine pathogens. Also of importance are the different kinds of tissue damage seen in autoimmune diseases. In general terms the reactions may be classified into four types, although they do not occur in isolation from each other: type I, **immediate hypersensitivity**; type II, **antibody-mediated hypersensitivity**; type III, **immune complex-mediated hypersensitivity**; and type IV, **delayed hypersensitivity**.

hypersharpening the formation of a 'sharper' boundary in sedimentation and moving boundary electrophoresis experiments than would be expected as a result of diffusion-broadening, because molecules in the trailing portion of the boundary tend to move at a greater velocity per unit field than molecules on the leading edge or in the plateau region.

hypertension the state or condition of having a higher than normal arterial blood pressure. —**hypertensive** *adj.*

hyperthyroidism *or* **thyrotoxicosis** a clinical state resulting from excessive secretion of thyroid hormones. The most common cause is Graves' disease; other causes include goitre and solitary toxic adenoma. The clinical manifestations include nervousness, irritability, fatigue, and heat intolerance; exophthalmia is present in some cases. Most symptoms derive from exaggeration of normal responses to thyroid hormones. *See also* **thyroxine**. —**hyperthyroid** *adj.*

hypertonic **1** *(of a solution)* having a higher osmotic pressure than that of some given solution, especially that of the fluid in or surrounding a given type of cell or a body fluid. **2** *(of a muscle)* showing or characterized by excessive tone or tension. *Compare* **hypotonic**. —**hypertonicity** *n.*

hypertriglyceridemia *or (esp. Brit.)* **hypertriglyceridaemia** *see* **hyperlipidaemia**.

hypertrophy the increase in the size of a tissue or organ resulting from an increase in the size of the cells present. *Compare* **hyperplasia**. —**hypertrophic** *adj.*

hyperuricemia *or (esp. Brit.)* **hyperuricaemia** the presence of abnormally high amounts of uric acid in the blood. This may be due to increased purine synthesis arising from a metabolic disorder, inherited or otherwise, or it may be due to reduced excretion – this may result from renal disease, the effect of drugs (e.g. salicylates) on the kidney, or the presence of organic acids (e.g. lactate) that competitively inhibit urate excretion. Hyperuricemia is associated with **gout**.

hypervariable regions regions in an **immunoglobulin** molecule where the amino-acid residues show a high degree of variation between one molecule and another. There are three hypervariable regions, two in the **V region** and one in the **D region**.

hypo *a common name for* sodium thiosulfate, especially when used in photographic processing.

hypo+ *or (before a vowel)* **hyp+** *prefix* denoting under, beneath, below, less than, or in deficit; below the normal range. *Compare* **hyper+**, **normo+**.

hypoalphalipoproteinemia *see* **hypolipoproteinemia**.

hypobaric of, relating to, or operating at pressures lower than normal.

hypobetalipoproteinemia *see* **hypolipoproteinemia**.

hypocalcemia *or (esp. Brit.)* **hypocalcaemia** the presence of a lower than normal concentration of **calcium** in the blood. It

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may be associated with disorders of vitamin D metabolism, **hypoparathyroidism**, magnesium deficiency, or pancreatitis. Clinical features include behavioural disturbances, stupor, numbness, paresthesia, muscle cramps or spasms, and convulsions. —**hypocalcemic** *or* **hypocalcaemic** *adj.*

hypocapnia *or* **hypocarbia** the presence of less than the normal amount of carbon dioxide in a vertebrate or in its blood. *Compare* **hypercapnia**. —**hypocapnic** *or* **hypocarbic** *adj.*

hypochlorhydria the presence of less than the normal amount of hydrochloric acid in the gastric juice. —**hypochlorhydric** *adj.*

hypocholesterolemia *or (esp. Brit.)* **hypocholesterolaemia** the presence of a lower than normal concentration of cholesterol in the blood. —**hypocholesterolemic** *or* **hypocholesterolaemic** *adj.*

hypochromatic **1** of, relating to, or exhibiting **hypochromatism**. **2** *an alternative word for* **hypochromic** (def. 1).

hypochromatism the condition or property (of a cell or cell organelle) of staining less intensely than normal; the presence of an abnormally low amount of chromatin.

hypochromic **1** *or* **hypochromatic** less highly coloured than normal; weakly coloured. **2** of, pertaining to, exhibiting, or resulting from **hypochromism**. **3** *(of a substance)* displaying a **hypochromic effect**. **4** describing erythrocytes that contain, or appear to contain, less hemoglobin than normal.

hypochromic effect the observed decrease in absorption of certain frequencies of electromagnetic radiation by solutions of some macromolecules when the structure of the molecules becomes more ordered.

hypochromicity a measure of the decrease in absorption of electromagnetic radiation at a specific wavelength, usually that of the absorption maximum, due to **hypochromism**.

hypochromism the decreased absorption of electromagnetic radiation exhibited by an ordered structure below that predicted on the basis of its constitution.

hypoglycemia *or (esp. Brit.)* **hypoglycaemia** the presence of an abnormally low blood glucose concentration, especially in relation to the fasting value. *See also* **glycemia**. —**hypoglycemic** *or* **hypoglycaemic** *adj.*

hypoglycin *or* **hypoglycine A** β-(methylenecyclopropyl)alanine; 2-amino-3-(methylenecyclopropane)propanoic acid. A nonprotein α-amino acid identified as the hypoglycemic and toxic principle of the unripe fruit of the **ackee** (*Blighia sapida*), where it is present both in the fleshy aril and in the seeds. In the latter it occurs also as the *N*-L-glutamyl derivative, **hypoglycin B**. Certain other fruits also contain hypoglycin. It is degraded in animals to methylenecyclopropylacetate, either free or conjugated to glycine or coenzyme A. Methylenecyclopropylacetyl-CoA is a potent and specific inhibitor of the oxidation of short-chain acyl-CoAs, particularly of butyryl-CoA. In hypoglycin poisoning butyryl-CoA undergoes hydrolysis to yield free butyrate, which accumulates in the blood to abnormal concentrations. *See also* **Jamaican vomiting sickness**.

Hyp(3-OH) *symbol for* a residue of the α-amino acid 3-hydroxy-L-proline (alternative to 3Hyp or Hyp). *See* **hydroxyproline**.

Hyp(4-OH) *symbol for* a residue of the α-amino acid 4-hydroxy-L-proline (alternative to 4Hyp or Hyp). *See* **hydroxyproline**.

hypokalemia *or (esp. Brit.)* **hypokalaemia** the presence in the blood of an abnormally low concentration of potassium. It may result from alkalosis, insulin administration, primary or secondary aldosteronism, or administration of drugs that are aldosterone antagonists. —**hypokalemic** *or* **hypokalaemic** *adj.*

hypolipoproteinemia the partial or total absence of any lipoprotein, or the presence of a defective lipoprotein, in the plasma. Several types of this condition are recognized. **Hypobetalipoproteinemia** is arbitrarily defined as a low density lipoprotein (LDL) cholesterol level below the fifth percentile for a given sex- and age-matched population. Such patients also have low triacylglycerol levels. In this condition, LDL cholesterol is always detectable, in contrast to homozygous **abetalipoproteinemia**, in which it is entirely absent. Hypobetalipoproteinemia appears to be due to a low rate of synthesis of LDL from very-low-density lipoprotein. Abetalipoproteinemia is a rare autosomal recessive disorder. It probably results from an abnormality in the synthesis or secretion of apo B, and it is accompanied by fat malabsorption, as chylomicron formation requires apo B. In the homozygote, levels of triacylglycerols, cholesterol, and phospholipids are extremely low. Heterozygotes may present with hypobetalipoproteinemia. **Hypoalphalipoproteinemia** is in some cases familial, and may result from defective apo A-I. In another disorder, known as fish-eye disease (due to severe corneal opacity) the structure of apo A-I is normal, but high-density lipoprotein (HDL) levels are only 10% of normal. In analphalipoproteinemia, or **Tangier disease**, HDL is virtually absent.

hyponatremia *or (esp. Brit.)* **hyponatraemia** the presence in the blood of an abnormally low concentration of sodium. It can occur as a result of incorrect administration of fluid intravenously or in parenteral feeding, after administration of diuretics, in congestive heart failure, or in protein imbalance. —**hyponatremic** *or* **hyponatraemic** *adj.*

hypoparathyroidism underactivity of the **parathyroid glands**.

hypophase the lower layer of a two-phase system. *Compare* **epiphase**. —**hypophasic** *adj.*

hypophosphatemia *or (esp. Brit.)* **hypophosphataemia** the presence of an abnormally low level of phosphate in the blood. It occurs in vitamin D deficiency, primary **hyperparathyroidism**, incorrect parenteral nutrition, and during recovery from diabetic ketoacidosis.

hypophysectomy surgical removal of the pituitary gland (i.e. hypophysis). —**hypophysectomize** *or* **hypophysectomise** *vb.*

hypophysiotropic factor *or* **hypophysiotropic hormone** *an alternative name for* **hypothalamic (regulatory) factor**.

hypophysis *or* **hypophysis cerebri** *an alternative name for* **pituitary gland**. *See also* **adenohypophysis**, **neurohypophysis**. —**hypophyseal** *or* **hypophysial** *adj.*

hypopituitarism total or (more often) partial loss of pituitary function, usually due to destructive lesions of the pituitary.

hypoplasia underdevelopment or defective formation of an organ or tissue. —**hypoplastic** *adj.*

hypoprothrombinemia *or (esp. Brit.)* **hypoprothrombinaemia** the presence of abnormally low (inadequate) levels of plasma prothrombin (factor II). It is commonly linked with vitamin K deficiency.

hyposecretion lesser than normal secretion by any endocrine or exocrine gland.

hypotension the state or condition of having a lower than normal arterial blood pressure. —**hypotensive** *adj.*

hypothalamic (regulatory) factor *or* **hypothalamic hormone** *or* **hypophysiotropic factor** *or* **hypophysiotropic hormone** any peptidic substance that is synthesized in the mammalian hypothalamus and released into the hypophyseal–portal circulation in response to neural and/or chemical stimuli, and that regulates the secretion (and perhaps also the synthesis) of a specific polypeptide hormone by the anterior lobe of the pituitary gland (i.e. adenohypophysis). These specific factors may be either releasing or release-inhibiting factors (or hormones); their recommended names are now formed by replacing the word-ending 'tropin' (or '-in' in prolactin) in the name of the corresponding pituitary hormone by the word-ending '-liberin' (for a releasing factor) or '-statin' (for a release-inhibiting factor).

hypothalamus (*pl.* **hypothalami**) the region of the vertebrate brain lying below the thalamus and around the floor of the third ventricle, just posterior to the attachment of the cerebral hemispheres. It lies just above the **pituitary gland**, to which it supplies various **hypothalamic (regulatory) factors**. —**hypothalamic** *adj.*

hypothyroidism deficient secretion by the thyroid gland, for whatever reason. In infants it leads to cretinism; in adults the consequences include low metabolic rate, lethargy, menstrual disorders, and in extreme cases **myxedema**. —**hypothyroid** *adj.*

hypotonic **1** (of a solution) having a lower osmotic pressure

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than that of some given solution, particularly the fluid in or surrounding a given type of cell or a body fluid. **2** (of a muscle) showing or characterized by diminished tone or tension. *Compare* **hypertonic**. —**hypotonicity** *n.*

hypovolemia *or (esp. Brit.)* **hypovolaemia** a reduction in the volume of circulating blood. It may be due to hemorrhage or to redistribution of fluid from the plasma to the extravascular tissues and spaces.

hypox *abbr. for* hypophysectomized. *See* **hypophysectomy**.

hypoxanthine *symbol*: Hyp; purin-6(1*H*)-one; 6-hydroxy purine; an intermediate in the degradation of adenylate. Its ribonucleoside is known as **inosine** and its ribonucleotide as **inosinate**. *Compare* **xanthine**. *See also* **hypoxanthine phosphoribosyltransferase**.

hypoxanthine–guanine phosphoribosyltransferase *abbr.*: HGPRT; *see* **hypoxanthine phosphoribosyltransferase**.

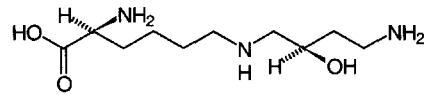
hypoxanthine phosphoribosyltransferase EC 2.4.2.8; *systematic name*: IMP: pyrophosphate phospho-D-ribosyltransferase; *other names*: hypoxanthine–guanine phosphoribosyltransferase (*abbr.*: HGPRT); IMP pyrophosphorylase. An enzyme that catalyses a reaction between 5-phospho-α-D-ribose 1-diphosphate and either hypoxanthine or guanine to form IMP or GMP respectively, with release of pyrophosphate. It is an enzyme of the purine salvage pathway, and a deficiency is associated with **Lesch-Nyhan syndrome** and **gout**. Example from human: database code HPRT_HUMAN, 217 amino acids (24.45 kDa); many mutations leading to deficiency diseases have been identified.

hypoxia the presence of less than normal amounts of dioxygen in a vertebrate or in its blood. *Compare* **hyperoxia**. —**hypoxic** *adj.*

Hypro *(formerly) symbol for* a residue of (4-)hydroxy-L-proline (4Hyp or Hyp now recommended).

hypsochromic describing the shift of an absorption band in the direction of shorter wavelengths. *Compare* **bathochromic**.

hypusine N^{ε}-[4-amino-2-hydroxybutyl]lysine; an amino acid uniquely formed by post-translational modification of one of the lysyl residues of eukaryotic translation initiation factor 5A (eIF-5A). It is formed by deoxyhypusine synthase, an enzyme that transfers the butylamine portion of spermidine to the ε-NH_2 group of a specific lysine of the eIF-5A precursor, followed by addition of the hydroxyl group by deoxyhypusine hydroxylase.



hysteresis the delay between the effect on a system and the cause producing the effect. —**hysteretic** *adj.*

hysteretic enzyme any enzyme that responds slowly (in terms of some kinetic characteristic) to a rapid change in ligand (either substrate or modifier) concentration. Such slow changes, defined in terms of their rates relative to the overall catalytic reaction, result in a lag in the response of the enzyme to changes in the ligand level.

Hz *symbol for* hertz.

H zone *see* **sarcomere**.

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I i

i *symbol for* **1** iso (def. 3); (as a prefix or superscript in symbols and abbreviations for iso compounds or groups; e.g. isopropyl can be symbolized as iPr or Pr^{i}). **2** the chemical group 2-isopentenyl; 3,3-dimethylallyl (as a prefix to a single-letter symbol for a nucleoside residue to designate substitution of the base, as in **i**A). **3** the square root of −1.

i *symbol for* **1** electric current (alternative to *I*). **2** van't Hoff factor.

I *symbol for* **1** iodine. **2** an iodo group in an organic compound. **3** a residue of the α-amino acid L-isoleucine (alternative to Ile). **4** a residue of the ribonucleoside inosine (alternative to Ino).

I *symbol for* **1** electric current (preferred alternative to *i*). **2** intensity; the subscripts e (for energetic), p (for photon), or v (for visible) may be added to distinguish between radiant intensity, photon intensity, and luminous intensity, respectively. **3** ionic strength; the subscripts c or m may be added to indicate whether it is expressed based on concentration or molality respectively. **4** the inductive effect of a particular chemical group in an organic compound.

iA *symbol for* N^6-(2-isopentenyl)adenosine, a **hypermodified base**.

IAA *abbr. for* indole-3-acetic acid *or* **indoleacetate**.

IAN *abbr. for* indoleacetonitrile.

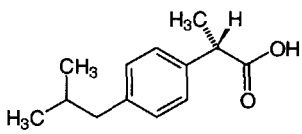
IAP *abbr. for* islet-activating protein; *see* **pertussis toxin**.

iatrogenic describing a condition or disease induced unintentionally by a physician through his or her diagnosis, manner, or therapy. —**iatrogenicity** *n.*

I-band *abbr. for* isotropic band. The I-bands of striated muscle contain the **thin filaments** and correspond to the light bands. The name derives from the fact that they are isotropic in polarized light. *See also* **sarcomere**.

IBMX *abbr. for* isobutylmethylxanthine.

ibuprofen 2-(4-isobutylphenyl)propionic acid; a nonsteroidal anti-inflammatory agent of the substituted propionic acid type; others of this type are flurbiprofen, **ketoprofen**, and naproxen. They inhibit the cyclooxygenase activity of **prostaglandin-endoperoxide synthase**, reversibly over short time intervals, followed by time-dependent irreversible inactivation, due probably to conformational rather than covalent changes. The racemic mixture is present in many over-the-counter drugs, but the (*S*)-enantiomer is the active form. *Proprietary names include*: Advil; Brufen; Motrin.



(*S*)-ibuprofen

ic *or* **i.c.** *abbr. for* intracutaneous or intracutaneously.

IC *abbr. for* internal conversion.

IC$_{50}$ **1** the median inhibitory concentration (in mol L^{-1}) of an antagonist, i.e. the concentration that reduces a specified response to 50% of its former value; *compare* **EC$_{50}$**. **2** the median inhibitory concentration (in mol L^{-1}) of an agent (agonist or antagonist), i.e. the concentration that causes a 50% reduction in the specific binding of a radioligand.

ICAM *abbr. for* intercellular adhesion molecule; any of several type I membrane glycoproteins of the immunoglobulin superfamily. They act as ligands for leukocyte adhesion to target cells, in conjunction with **LFA-1**; in fact LFA-1–ICAM links mediate adhesion between many cell types. There are three subclasses. **ICAM-1** (*or* CD54), of molecular mass 90–115 kDa, are expressed on B and T cells, endothelial, epithelial, and dendritic cells, fibroblasts, keratinocytes, and chondrocytes. They are inducible in 12–24 hours by cytokines such as gamma interferon, interleukin-1β, and tumour necrosis factor-α. Example (human, precursors): ICAM-1 major group rhinovirus receptor: database code ICA1_HUMAN, 532 amino acids (57.76 kDa). **ICAM-2** (*or* CD102), of molecular mass 55–65 kDa, are constitutively expressed on endothelial cells, some lymphocytes, monocytes, and dendritic cells. Example (human): database code ICA2_HUMAN, 275 amino acids (30.62 kDa). **ICAM-3** (*or* CD50), of molecular mass 116–140 kDa, are constitutively expressed on monocytes, granulocytes, and lymphocytes; upon physiological stimulation they become rapidly and transiently phosphorylated on serine residues. Example (human): database code ICA3_HUMAN, 547 amino acids (59.32 kDa).

ICD *(in clinical chemistry) abbr. for* isocitrate dehydrogenase (EC 1.1.1.41).

ice the solid form of water that can exist at temperatures below the triple point of water (273.16 K at 101 325 Pa).

iceberg a metaphor used to describe an interpretation of the anomalous entropies of solution of noble gases and other nonpolar substances in water, suggesting that water tends to organize itself into quasi-solid supramolecular structures around the molecules of such substances. In the case of alkyl compounds, this tendency increases markedly with the length of the alkyl chain.

ICE-like protease any of a family of endopeptidases that structurally resemble **interleukin-1β convertase** (ICE). They are involved in **apoptosis**, being implicated in the proteolysis that causes cell death.

I cell **1** *or* **CCK cell** any of a group of cells, widely distributed in the duodenal and jejunal mucosa, that produce **cholecystokinin**. So named because their histological features are intermediate between those of **S cells** and **L cells**. **2** *abbr. for* inclusion cell. *See also* **I-cell disease**.

I-cell disease *or* **inclusion-cell disease** *or* **mucolipidosis II** an autosomal recessive disease in which most of the lysosomes in the connective tissue (fibroblasts) contain large inclusions of glycoaminoglycans and glycolipids as a result of the absence of several lysosomal hydrolases. These enzymes, which are synthesized in the endoplasmic reticulum, are secreted into the extracellular medium rather than being directed to the lysosomes. This is due to the absence of a mannose 6-phosphate marker on the carbohydrate moieties of these hydrolases because of a deficiency in an enzyme required for mannose phosphorylation. The failure of the phosphorylation in the *cis* Golgi network means that the enzymes are not segregated by the **mannose 6-phosphate receptors** into the appropriate transport vesicles in the *trans* Golgi network. The patients have an abnormally high level of lysosomal enzymes in their sera and body fluids. A milder form of I-cell disease is Hurler's polydystrophy (**Hurler syndrome**).

ice point the temperature at which ice melts. It is taken as the temperature (273.15 K) at which ice and water are in equilibrium at standard pressure (101 325 Pa). It was used as a reference temperature on the Celsius scale, but the kelvin is based instead on the temperature at the **triple point** of water (273.16 K).

ICF *abbr. for* intracellular fluid.

ichthyotocin *an alternative name for* **isotocin**.

icosa+ *or (before a vowel)* **icos+** *comb. form* recommended for denoting twenty or twenty times. *Also (formerly)*: **eicosa+**, **eicos+**. (*Note*: the eicos(a)+ variant is still always used for the C_{20} fatty acids and skeletally related compounds, e.g. the eicosanoids.)

icosadeltahedron (*pl.* **icosadeltahedra**) any solid geometrical

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figure obtained by dividing the triangular faces of an **icosahedron** into smaller triangles. If divided into more than four smaller triangles, the original faces will not be flat, in which case the 12 pentameric vertices will be supplemented by hexameric vertices. —**icosadeltahedral** *adj.*

icosahedral symmetry a form of **cubic symmetry**, being the crystallographic symmetry displayed by an **icosahedron** and by the capsid of some types of virus.

icosahedron (*pl.* **icosahedra**) any solid geometrical figure having 20 triangular faces, 30 edges, and 12 pentameric vertices. A regular icosahedron has faces that are congruent plane equilateral triangles; there is twofold rotational symmetry about an axis through the midpoint of each edge, threefold rotational symmetry about an axis through the centre of each face, and fivefold rotational symmetry about an axis through each vertex. —**icosahedral** *adj.*

icosanoate *or (formerly)* eicosanoate *the systematic name for* **arachidate**.

icosanoid *the recommended name for* **eicosanoid**, but not generally used.

ICRO *abbr. for* International Cell Research Organization.

ICSH *abbr. for* interstitial cell-stimulating hormone (i.e. **luteinizing hormone**).

ICSU *abbr. for* International Council of Scientific Unions.

icterus *(in pathology) an alternative name for* **jaundice**.

icterogenic causing **jaundice**.

id *or* **i.d.** *abbr. for* **1** intradermal, or intradermally (alternative to ID). **2** inside diameter.

ID **1** *(in clinical chemistry) abbr. for* iditol dehydrogenase (EC 1.1.1.14). **2** *abbr. for* intradermal, or intradermally (alternative to id).

ID_{50} *or* **ID50** *abbr. for* median infectious dose.

idaric acid the **aldaric acid** derived from idose.

IDDM *abbr. for* insulin-dependent diabetes mellitus (*see* **diabetes mellitus**).

+ide *suffix (in chemical nomenclature)* denoting a **lactide**. It replaces the terminal '+ic acid' of the trivial name of the parent hydroxy acid, and a multiplying prefix indicates the number of molecules of hydroxy acid involved; e.g. dilactide (formed from two molecules of lactic acid).

ideal describing any object, process, or system that is perfect, or that behaves exactly in accordance with some simple law or theory. *See also* **ideal gas**, **ideal solution**. —**ideality** *n.*

ideal gas any gas whose behaviour is accurately described by the **gas laws**.

ideal solution any solution in which, for each component,

$$d\mu_i = RT\, d\ln x_i,$$

where μ_i is the chemical potential of the ith component and x_i is its mole fraction, R is the universal gas constant, and T is the thermodynamic temperature. Integration of the above equation gives:

$$\mu_i = \mu_i^{\circ} + RT \ln x_i,$$

where μ_i° is the standard chemical potential of the ith component.

idio+ *comb. form* denoting **1** peculiar, distinct, one's own, separate. **2** self-produced, arising within.

idiogram *or* **karyogram** a diagrammatic representation of the **karyotype** of a cell, based on measurement of the chromosomes in several or in many cells.

idiom *(in immunology)* the group of **idiotypes** to which the **epitopes** carried by components of one individual animal belong.

idiopathic **1** *(in pathology)* describing a disease arising by itself, not consequent upon, or symptomatic of, another disease; of the nature of a primary morbid state; essential. **2** of the nature of a particular affection or susceptibility. —**idiopathy** *n.*

idiopathic pentosuria *see* **pentosuria** (def. 1).

idiotope **1** the group of **epitopes** carried by components of one individual animal. **2** as originally defined by **Jerne**, an individual determinant (i.e. site) on an antibody molecule; together, the idiotopes constitute the idiotype.

idiotype **1** an antigenic specificity, particularly of antibodies directed against a single antigen. **2** any class or group of related antigenic characteristics or **idiotopes**; an **epitype** that is characteristic of a particular animal. —**idiotypic** *adj.*

iditol the hexitol derived formally by reduction of the aldehyde group of idose. L-Iditol is a rare natural product accompanying sorbitol in the fermented juice of berries of mountain ash (*Sorbus aucuparia*).

IDL *abbr. for* intermediate-density lipoprotein.

iDNA *abbr. for* intercalary DNA.

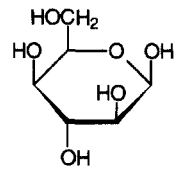
IDNPAP *abbr. for* isethionyl-3-(*N*-2,4-dinitrophenyl)amino propioimidate; a reagent useful in the isolation of plasma membranes. It reacts with, but does not penetrate, the membranes and leaves the net charge on the proteins unaltered.

ido- *prefix (in chemical nomenclature)* indicating a particular configuration of a set of four (usually) contiguous >CHOH groups, as in the acyclic form of D- or L-idose. *See* **monosaccharide**.

Ido *symbol for* a residue (or sometimes a molecule) of the aldohexose idose.

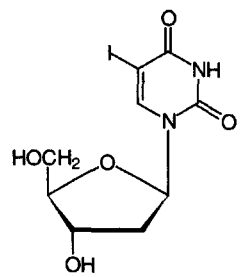
IdoA *symbol for* a residue of iduronic acid.

idose *symbol*: Ido; *ido*-hexose; an aldohexose whose D- and L-enantiomers are epimeric at C-2, C-3, and C-4 with D- and L-glucose, respectively.



β-D-idose

idoxuridine 5-iodo-2′-deoxyuridine; a pyrimidine analogue, metabolized to the triphosphate, that inhibits DNA replication by substituting for thymidine in viral and mammalian DNA incorporation. It is used as an antiviral agent.



IDP *abbr. for* **1** the ribonucleotide inosine (5′-)diphosphate. **2** isopentenyl diphosphate (*formerly called* Δ^3-isopentenyl pyrophosphate).

IDU *abbr. for* 5-iodo-2′-deoxyuridine (*see* **idoxuridine**).

IdUrd *symbol for* 5-iodo-2′-deoxyuridine (*see* **idoxuridine**) (preferred to IDU, IUdR, or IUDR).

iduronate **1** the anion of **iduronic acid**. **2** any salt or ester of iduronic acid.

iduronate-2-sulfatase EC 3.1.6.13; *other name*: chondroitin-sulfatase; an enzyme that hydrolyses the 2-sulfate groups of the L-iduronate 2-sulfate units of dermatan sulfate, heparan sulfate, and heparin. Example (precursor) from human: database code IDS_HUMAN, 550 amino acids (61.80 kDa).

iduronic acid *symbol*: IdoA; the **uronic acid** formally derived

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from idose by oxidation to a carboxyl group of the hydroxymethylene group at position 6. In nature α-linked L-iduronic-acid residues, sulfated at position 2, occur in terminal positions in dermatan sulfate and heparan sulfate; these iduronic-acid residues are formed by epimerization of the configuration at C-5 of D-glucuronic-acid residues in these heteropolysaccharides.

L-iduronidase EC 3.2.1.76; an enzyme that hydrolyses α-L-iduronosidic linkages in desulfated dermatan. Example (precursor) from human: database code IDUA_HUMAN, 653 amino acids (72.58 kDa).

iduronosyl the glycosyl group formed by removal of the anomeric hydroxyl group from **iduronic acid** or iduronate.

IE *abbr. for* immunoelectrophoresis (alternative to IEP).

IEC *abbr. for* ion-exchange cellulose.

IED *abbr. for* individual effective dose. IED_{50} denotes the median of the IEDs within a group of subjects.

IEF *abbr. for* isoelectric focusing.

IEP *abbr. for* **1** immunoelectrophoresis (alternative to IE). **2** *or* **i.e.p.** isoelectric point (pI preferred).

IF *abbr. for* initiation factor. Suffixed numerals are added to designate individual factors, e.g. **IF-1**, **IF-2**, IF-2a, **IF-3**. Eukaryotic initiation factors are generally denoted by the prefix 'e', e.g. eIF-2, eIF-3.

IF-1 an *Escherichia coli* **initiation factor**.

IF-2 an *Escherichia coli* **initiation factor**.

IF-3 an *Escherichia coli* **initiation factor**.

IFCC *abbr. for* International Federation of Clinical Chemistry.

IFN *abbr. for* interferon. Suffixed Greek letters are added to differentiate the main classes, e.g. IFN-α, IFN-β, IFN-γ.

Ig *symbol for* immunoglobulin.

IgA *symbol for* immunoglobulin A.

IgA protease *another name for* **IgA-specific serine endopeptidase**.

IgA-specific serine endopeptidase EC 3.4.21.72; *other name*: IgA protease; an enzyme that catalyses the cleavage of immunoglobulin A molecules at certain Pro-|-Xaa bonds in the hinge region. No small molecule substrates are known. It is an excreted bacterial serine proteinase. A signal peptide guides the enzyme precursor to the periplasmic space, and the C-terminal helper domain associates with the outer membrane to form a pore for excretion of the protease domain. The helper domain is then released by autoproteolysis. Example from *Neisseria gonorrhoeae*: database code IGA_NEIGO, 1532 amino acids (168.79 kDa).

IG cell the intestinal gastrin cell, a small, granulated, gastrin-producing cell occurring in the human upper small intestine. IG cells react both with gastrin-specific antisera and with antisera recognizing the C-terminal pentapeptide sequence common to gastrin and cholecystokinin (CCK). IG cells are smaller than, and ultrastructurally different from, CCK-producing **I cells**, gastrin-producing **G cells** of the gastric pylorus, and **TG cells**.

IgD *symbol for* immunoglobulin D.

IgE *symbol for* immunoglobulin E.

igensin a neutral cytosolic serine proteinease, activated by sodium dodecyl sulfate and found in a number of mammalian tissues.

IGF *abbr. for* insulin-like growth factor.

IGFBP *abbr. for* insulin-like growth factor binding protein.

IgG *symbol for* immunoglobulin G. Suffixed numerals are added to designate individual subclasses, e.g. IgG1, IgG2, IgG3, IgG4.

Ig-like domain *see* **immunoglobulin fold**.

IgM *symbol for* immunoglobulin M.

βIG-M1 *see* **connective tissue growth factor**.

βIG-M2 *see* **connective tissue growth factor**.

ignose the name first proposed for ascorbic acid by A. Szent-Györgyi, before he knew its structure. *See also* **godnose**, .

IGT *abbr. for* impaired glucose tolerance.

Ii system a blood group system in which the antigenic determinant is an oligosaccharide structure. It is structurally related to the ABH system (*see* **ABH antigens**), anti-I and anti-i antibodies being inhibited by ABH and Lewis glycoproteins. Anti-I and anti-i are the major **cold autoantibodies**; the anti-I factors occur in the transient anemia accompanying viral or *Mycoplasma pneumoniae* infections; the i-specific antibodies are characteristic of the so-called chronic cold agglutinin disease, accompanying chronic lymphoproliferative diseases of the non-Hodgkin type. The structures of the determinants are: i determinant, GlcNAc(β1-3)Gal(β1-4)GlcNAcβ1-R; I determinant, Gal(β1-4)[Gal(β1-4)GlcNAc(β1-6)]GlcNAc(β1-3)Gal(β1-4)GlcNAcβ1-R.

ikaros a protein that binds and activates the **enhancer** of a gene *CD3*-δ involved in T-lymphocyte specification and maturation. Similar to **hunchback**, it is a zinc-finger protein. Example from mouse: database code IKAR_MOUSE, 431 amino acids (48.13 kDa).

IL *abbr. for* interleukin. Various distinct interleukins are distinguished by suffixed numerals, e.g. IL-1, IL-2, IL-3, etc.

ILA *abbr. for* insulin-like activity.

Ile *symbol for* a residue of the α-amino acid L-isoleucine (alternative to I).

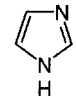
ileum the lower part of the small intestine, extending from the jejunum to the large intestine. —**ileal** *adj.*

illegitimate transcription transcription at a low level of a normally tissue-specific transcribing gene in nonspecific cells.

IM *or* **i.m.** *abbr. for* intramuscular, or intramuscularly.

imidate **1** any salt or ester of an **imidic acid**. **2** to convert an oxo diacid into its corresponding **imide**. —**imidation** *n.*

imidazole *or (formerly)* **glyoxaline** *or* **iminazole** 1,3-diazole; 1,3-diaza-2,3-cyclopentadiene; a weak base, pK_a ≈6.95. The numbering and tautomerism of the imidazole ring are described at **histidine**.



imidazole 4-acetate a product of histamine metabolism; it results from the action of monoamine oxidase on histamine to form imidazole 4-acetaldehyde, which is then oxidized by an NAD^+-dependent aldehyde dehydrogenase to imidazole 4-acetate. *See also* **histidine**.

imidazoline receptor any of a class of mitochondrial or plasma membrane binding sites for compounds from the generic groups imidazoles, imidazolines, imidazolidines, guanidines, and oxazolines, and having a putative endogenous ligand, **agmatine**. They occur throughout the brain, where they are possibly associated with glial cells, and in peripheral tissues. Two subtypes (at least) have been characterized pharmacologically: **I_1 receptors**, which have high affinity for *p*-aminoclonidine and are localized in plasma membranes, and **I_2 receptors**, which have high affinity for idazoxan and are localized in mitochondrial membranes. The latter are known alternatively as nonadrenergic imidazoline binding sites (NAIBSs). Photoaffinity labelling to at least three proteins occurs: two, of M_r 55 000 and 61 000, are found in rat liver and differ in their binding affinity for the guanidium, amiloride; a third, of M_r 61 000, is found in PC-12 cells and has high affinity for amiloride but low affinity for idazoxan. These proteins may represent different I_2 receptors. Subtypes of I_2 receptors are also suggested pharmacologically. The function of imidazoline receptors is not yet known, but many of the effects of imidazoline compounds, formerly attributed to their binding to α_2 receptors (e.g. hypotension) are now attributed to NAIBSs.

imidazolium **1** the cation formed by addition of a proton (hydron) to a molecule of **imidazole**. **2** the cationic chemical group formed by addition of a proton (hydron) to an **imidazolyl** group.

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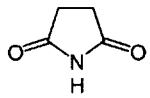
imidazolyl the chemical group derived formally by removal of one hydrogen atom from **imidazole**. The position from which the hydrogen atom has been removed may be indicated, e.g. 2-imidazolyl. The imidazolyl group is present in **histidine** and its derivatives.

imide any secondary organic amide (i.e. any diacyl derivative of ammonia or a primary amine), especially any that is a cyclic compound in which both of the acyl groups (which may be the same or different) are derived formally or actually from a diacid. (*Note*: Noncyclic symmetrical secondary organic amides are generically termed **diacylamines**.)

+imide *suffix (in chemical nomenclature)* designating any organic compound that is an **imide**. The nitrogen atom may be substituted with a named alkyl or other group. An example is succinimide:



succinimide

imidic acid any derivative of a carboxylic acid in which the carbonyl oxygen atom of the carboxyl group has been replaced by an **imino** (def. 1) or alkylimino group; i.e. any containing the –C(=NR)–OH group. *Distinguish from* **imino acid**.

imido+ *comb. form* designating any inorganic oxo acid (including the anions, salts, and esters) in which =O has been replaced by =NH or =NR (where R is a named substituent), or any derived di-, tri-, etc. acid in which a bridging oxygen atom, –O–, has similarly been replaced by –NH– or –NR–; e.g., **adenosine 5′-[β,γ-imido]triphosphate**.

Imigran *see* **sumatriptan**.

iminazole *a former name for* **imidazole**.

imine **1** any organic compound having the general structure $R_2C{=}NR$ where R may be any organyl group or H. *See also* **aldimine**, **azomethine**, **ketimine**, **Schiff base**. **2** *an obsolete term for* azacycloalkane.

iminium the bivalent quaternary nitrogen-containing cationic group $={}^{+}NR_2$ attached to carbon in a chemical compound, where the R groups may each be hydrogen or any organyl group.

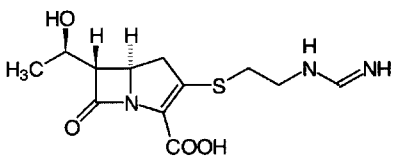
imino the bivalent group =NH attached to carbon in a chemical compound.

imino+ *comb. form* denoting the presence in a chemical compound of one or more **imino** groups; the number of imino groups in the molecule may be specified, e.g. diimino+.

imino acid any carboxylic acid in which an imino substituent replaces two hydrogen atoms. In biochemistry the term is commonly applied also to certain cyclic alkylamino (especially α-alkylamino) derivatives of aliphatic carboxylic acids, e.g. **proline**, although such compounds are now preferably classed as azacycloalkane carboxylic acids. *Compare* **imidic acid**.

iminodipeptidase *see* **Pro-X dipeptidase**.

imipenem a carbapenem β-lactam antibiotic that is a semisynthetic derivative of thienamycin produced by *Streptomyces cattleya*. Its broad-spectrum antibiotic actions resemble those of penicillins, i.e. inhibition of bacterial peptidoglycan synthesis.



immediate gene *or* **immediate-early gene** *see* **early gene**.

immediate hypersensitivity *or* **type I hypersensitivity** a type of **hypersensitivity** responsible for asthma, hayfever, and some types of eczema. It occurs within minutes of exposure to antigen and is dependent on the activation of **mast cells** and the release of mediators of acute inflammation. The mast cells bind **immunoglobulin E** (IgE) via their surface **Fc receptors** and when antigen cross-links the IgE, the mast cells degranulate releasing vasoactive amines that mediate the symptoms.

immobilize *or* **immobilise** to render any agent, whether a micro- or macrosolute, a particle, or an intact cell, nondispersible in an aqueous medium with retention of its specific ligating, antigenic, catalytic, or other properties. Immobilization may be achieved by, e.g., encapsulation, entrapment in a small-pore gel, adsorption on, or covalent linkage to, an insoluble supporting material (matrix), or through formation of aggregates by cross-linkage.

immobilized enzyme *see* **solid-phase technique**.

immortalization *or* **immortalisation** the **transformation** of a cell population with a finite life span to one possessing an infinite life span. It is a characteristic of cancer cells, and is of practical importance in, e.g., the creation of **monoclonal antibodies**. Immortalization of eukaryotic cells may be effected experimentally by infection with certain viruses, or by fusion of the cell with a neoplastic cell to form a **hybridoma**. —**immortalize** *or* **immortalise** *vb.*

immune **1** relating to or possessing **immunity**. **2** regarding or describing an animal that has been immunized. **3** *an alternative word for* **immunological**.

immune adherence the **complement**-dependent adherence of antibody–antigen complexes, or of antibody-coated bacteria (or other particles), to primate erythrocytes, causing the agglutination of the latter.

immune clearance *an alternative term for* **immune elimination**.

immune complex *an alternative term for* **antigen–antibody complex**.

immune complex-mediated hypersensitivity *or* **type III hypersensitivity** a type of **hypersensitivity** caused by the deposition of antigen–antibody complexes in tissue and blood vessels. The complexes activate **complement** and attract polymorphs and macrophages to the site.

immune cytolysis the **complement**-dependent lysis of cells by antibody molecules. When the cells concerned are erythrocytes the process is termed **immune hemolysis**.

immune elimination *or* **immune clearance** the accelerated, exponential removal of antigen from an immune animal as a result of complexing with antibody molecules.

immune globulin *(sometimes) an alternative name for* **immunoglobulin**.

immune hemolysis *see* **immune cytolysis**.

immune response the total immunological reaction of an animal to an immunogenic stimulus. It includes antibody formation, the development of hypersensitivity, and immunological tolerance.

immune serum *an alternative term for* **antiserum**.

immunity freedom and protection from 'infection'. Two forms of immunity can be recognized: (1) innate, meaning non-specific anti-microbial systems (e.g. phagocytosis) that are innate in that they are not intrinsically affected by prior contact with the infectious agent; and (2) the state of an animal that has an enhanced ability, above the nonimmune state, to respond to some (specific) antigen in which the antigen is bound and rendered inactive or eliminated from the body. *See also* **active immunity**, **passive immunity**.

immunization *or* **immunisation** any procedure carried out on an animal, e.g. the administration of antigen or antibody, that leads to an increased reactivity of the animal's immune system towards an antigen or antigens. —**immunize** or **immunise** *vb.*

immuno+ *comb. form* indicating immune or immunity.

immunoadsorbent any insoluble preparation of an antigen

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(or antibody) suitable for use in **immunoadsorption**. *See also* **immunosorbent**.

immunoadsorption the use of an insoluble antigen (or antibody) to remove specifically unwanted antibodies (or antigens) from a mixture so as to make the antibody (or antigen) more specific. *Compare* **adsorption** (def. 2). *See also* **immunosorption**.

immunoaffinity chromatography a type of **affinity chromatography** in which one of the two components of an antigen–antibody system is coupled to an insoluble matrix and used for the separation and purification of the other component.

immunoaffinity column a chromatographic column used in **immunoaffinity chromatography**.

immunoassay **1** any of a group of techniques for the measurement of specific biochemical substances, commonly at low concentrations and in complex mixtures such as biological fluids, that depend upon the specificity and high affinity shown by suitably prepared and selected antibodies for their complementary antigens. A substance to be measured must, of necessity, be antigenic – either an immunogenic macromolecule or a haptenic small molecule. To each sample a known, limited amount of specific antibody is added and the fraction of the antigen combining with it, often expressed as the bound:free ratio, is estimated, using as indicator a form of the antigen labelled with a radioisotope (**radioimmunoassay**), fluorescent molecule (**fluoroimmunoassay**), stable free radical (**spin immunoassay**), enzyme (**enzyme immunoassay**), or other readily distinguishable label. The amount of the antigen in the sample is found by comparison with standards containing known amounts. *See also* **heterogeneous immunoassay**, **homogeneous immunoassay**, **saturation analysis**. **2** *an alternative name for* **radioimmunoassay**. **3** to carry out or to estimate (something) by an **immunoassay** (def. 1, 2).

immunobiology the branch of biology dealing with the activities of the cells of the immune system and their relationship to each other and to their environment. —**immunobiological** *adj.*

immunochemical **1** of or relating to **immunochemistry**. **2** any specific immunological reagent that consists of or incorporates an antigen or an antibody, especially one of commerce.

immunochemistry the branch of biochemistry dealing with the chemical nature of antigens, antibodies, and their interactions, and with the chemical methods and concepts as applied to immunology.

immunochromatogram the pattern of precipitation bands formed in **immunochromatography**.

immunochromatography any of various techniques for separating and identifying soluble antigens. In one method, analogous to **immunoelectrophoresis**, the antigens are first fractionated through a thin-layer chromatogram, e.g. of Sephadex; the fractions are then diffused against a trough containing a solution of antibodies (antiserum). In another method a small drop of antigen–antiserum mixture is applied to filter paper, or resin-impregnated paper, and the chromatogram developed with buffer; any antigen–antibody complex remains at the point of application and can be detected with a protein stain, while the other proteins are washed away from the origin.

immunocompetent cell an immunologically competent cell.

immunocyte any **immunologically competent cell**.

immunocytochemistry **cytochemistry** using appropriately labelled antibody preparations to detect specific cellular components. —**immunocytochemical** *adj.*

immunodeficiency any condition in which there is a deficiency in the production of humoral and/or cell-mediated immunity. —**immunodeficient** *adj.*

immunodeterminant *an alternative name for* **antigenic determinant**.

immunodiagnosis the diagnosis of disease by immunological methods.

immunodiagnostic **1** of or relating to **immunodiagnosis**. **2** any specific immunological reagent used in diagnosis.

immunodiffusion any of various analytical methods by which components of soluble antigen or antibody mixtures may be distinguished. Essentially, the antigens and antibodies are allowed to diffuse towards each other in a translucent gel, wherein they react to gives lines or bands of precipitation in characteristic positions. Such methods include: **double immunodiffusion**, **electroimmunodiffusion**, **immunochromatography**, **immunoelectrophoresis**, immunorheophoresis, and **single radial immunodiffusion**. —**immunodiffuse** *vb.*

immunodominance the attribute of a part of an **epitope** that contributes a disproportionately great portion of the binding energy; e.g. the immunodominance shown by a monosaccharide residue in determining the antigenic specificity of a polysaccharide. —**immunodominant** *adj.*

immunoelectrofocusing *or* **immunoisoelectric focusing** a technique that is analogous to **immunoelectrophoresis** but with the preliminary fractionation of one of the reactants being effected by electrofocusing instead of electrophoresis.

immunoelectron microscopy a form of electron microscopy in which structures are stained with specific antibodies labelled with an electron-dense material.

immunoelectropherogram *(sometimes)* the record of an immunoelectrophoresis experiment, either the electrophoretic support itself or a tracing derived therefrom.

immunoelectrophoresis *abbr.*: IE *or* IEP; a technique for separating and identifying soluble antigens. It consists of **zone electrophoresis**, in a reasonably transparent gel, in one direction followed by **immunodiffusion** against a solution of antibodies (antiserum) placed in a trough parallel to the direction of electrophoresis. In suitable conditions each antigen shows up as an arc of precipitation in a characteristic position. —**immunoelectrophoretic**, **immunoelectrophoretical** *adj.*

immunoenzymatic of or pertaining to the particular techniques used in **immunoenzymology**.

immunoenzymology the subspeciality of immunochemistry in which the activity of enzymes coupled to antigens or antibodies is utilized as a molecular amplifier of antigen–antibody reactions.

immunofixation *or* **immunofixation electrophoresis** a variant of **immunoelectrophoresis**, or **immunoelectrofocusing**, in which proteins of a single immunological species are anchored to the support by treatment with monospecific antibodies, allowing the other proteins to be washed out of the support. It is useful in the identification of proteins in complex mixtures or of minor proteins obscured in electrophoretic patterns.

immunofluorescence *or* **immunofluorescence microscopy** a technique in which an antigen or antibody is made fluorescent by conjugation to a fluorescent dye and then allowed to react with the complementary antibody or antigen in a tissue section or smear. The location of the antigen or antibody can then be determined by observing the fluorescence by microscopy under ultraviolet light. —**immunofluorescent** *adj.*

immunogelfiltration *a variant of* **radial single immunodiffusion** in which antigen is first fractionated according to its molecular size by permeation, in a buffer solution, into a thin layer of an appropriate cross-linked dextran gel. The dextran layer is then covered with a layer of agarose gel containing antibody. Rings or spots of antigen–antibody precipitate develop in the agarose gel over the complementary antigens.

immunogen **1** any substance that, when introduced into the body, elicits humoral or cell-mediated immunity, but not immunological tolerance. **2** any substance that is able to stimulate an immune response, as distinct from substances (antigens) that can combine with antibody. **3** any substance that is able to stimulate protective immunity against a pathogen, as distinct from an immune response that is of no intrinsic value to the animal immunized. —**immunogenic** *adj.*

immunogenetics *(functioning as sing.)* the branch of biology that combines immunology and genetics. It includes the use of immunological methods and knowledge in the study of genet-

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ics, and the use of genetics in the study of immunological phenomena and substances. —**immunogenetic** *adj.*

immunogenicity *an alternative term for* **antigenicity**.

immunoglobulin *symbol*: Ig; any member of a group of proteins occurring in higher animals as major components of the immune system. They are produced by cells of the lymphocyte series, and virtually all possess specific antibody activity. Each immunoglobulin molecule essentially comprises four polypeptide chains, two identical **heavy chains** and two identical **light chains**, linked together by disulfide bonds; all contain in addition differing amounts of attached oligosaccharide. There are five classes, IgA, IgD, IgE, IgG, and IgM. The primary structures of the heavy chains differ among the various classes, being designated α, δ, ε, γ, and μ, respectively for the classes listed above, and there are two types of light chain, κ and λ. IgA and IgM molecules contain multiples of the four-chain unit. The homology units form a characteristic motif, the **immunoglobulin fold**. *See also* **immunoglobulin A**, **immunoglobulin D**, **immunoglobulin E**, **immunoglobulin G**, **immunoglobulin M**.

immunoglobulin A *symbol*: IgA; an **immunoglobulin** found in human plasma, where its role is uncertain. It occurs mostly as a 170 kDa monomer of the basic four-chain immunoglobulin structure or, as a 400 kDa dimer, together with an extra 15 kDa polypeptide, the **J chain**, linked to **secretory piece**. It is the major immunoglobulin of seromucous secretions, in which it is concerned in the defence of external body surfaces against attack by microorganisms. It has the structure $(\alpha_2 l_2)_n J$, where α is the heavy chain, l is the light chain (κ or λ), J is the J chain, and *n* is 1 or 2. Example, α_1 C region: database code ALC1_HUMAN, 353 amino acids (37.61 kDa). *See also* **IgA-specific serine endopeptidase**.

immunoglobulin D *symbol*: IgD; a 185 kDa **immunoglobulin** that is very susceptible to proteolytic degradation and has a very short half-life in plasma. It is found in large amounts on the surface of B lymphocytes together with immunoglobulin M; it is probable that these two immunoglobulins function as mutually interacting antigen receptors and play a part in the control of lymphocyte activation and suppression. It has the structure $\delta_2 l_2$ where δ is the heavy chain and l is a light chain (κ or λ). Example, heavy chain (C region): database code DTC_HUMAN, 383 amino acids (42.08 kDa).

immunoglobulin E *symbol*: IgE; a 200 kDa **immunoglobulin** of high carbohydrate content, normally found in very low concentrations in plasma, although its concentration there is elevated in a number of allergic conditions. IgE is synthesized mainly in lymphoid tissue of gut and respiratory tract. It binds strongly to mast cells and contact with antigen leads to degranulation of the mast cells and release of inflammatory mediators. It has the structure $\varepsilon_2 l_2$ where ε is a heavy chain and l is a light chain (κ or λ). Example, heavy chain C region: database code EPC_HUMAN, 428 amino acids (46.97 kDa).

immunoglobulin fold a series of β strands, arranged as two antiparallel β sheets packed tightly against each other, that is highly characteristic of immunoglobulin structure. In the constant region, the two β sheets are formed from four and three β strands respectively. In the variable region there are nine β strands (five and four) rather than seven. This type of structure is found in many other proteins, especially cell surface receptors, and is often referred to as an **Ig-like domain**.

immunoglobulin G *symbol*: IgG; the principal **immunoglobulin** of human plasma and other internal body fluids. It is a 150 kDa protein and is the major immunoglobulin synthesized during the period of secondary response to an antigen. In the tissue fluids it neutralizes bacterial toxins and binds to microorganisms thereby enhancing their phagocytosis. Complexes of IgG with microorganisms activate **complement** by the classical pathway. IgG binds to macrophages and polymorphonuclear lymphocytes and can cross the placenta. It has the structure $\gamma_2 l_2$ where γ is a heavy chain and l is a light chain (κ or λ). There are subclasses of IgG depending on different types of γ chain. Example, IgG γ-1 C region: database code GC1_HUMAN, 330 amino acids (36.06 kDa); 3-D structure known.

immunoglobulin M *symbol*: IgM; a 900 kDa **immunoglobulin** consisting of a star-shaped polymer of five basic four-chain structures, each heavy chain bearing an extra constant domain. Polymerization is dependent on the presence of **J chain**, which may act to stabilize the sulfhydryl groups in the constant portion of the heavy chains during IgM synthesis. IgM is produced early in the immune response and is mainly found intravascularly. Because of its high antigen-combining valency it is very effective in binding microorganisms and mediating **complement**-dependent cytolysis. It has the structure $(\mu_2 l_2)_5 J$ where μ is a heavy chain, l is a light chain (κ or λ), and J is a J chain. Virgin B lymphocytes have an altered sequence at the C terminus of μ and the switch is effected by alternative splicing. Example, the protein from **heavy chain disease**, which has no C and $C_H 1$ regions due to deletion: database code MUCB_HUMAN, 391 amino acids (43.00 kDa).

immunoglobulin superfamily a superfamily of proteins that have similarities of sequence and structure to immunoglobulins. The superfamily has been divided into three sets, based on immunoglobulin domains: one with variable-like domains, the V set, and two with different variants of the constant-like domains, the C1 and C2 sets.

immunogram *(sometimes)* the pattern of bands or lines of precipitation formed in a gel by **immunodiffusion**.

immunohistochemistry a form of **histochemistry** in which appropriately labelled antibody preparations are used to detect specific structures in tissues. —**immunohistochemical** *adj.*

immunoliposome a **liposome** bearing a chemically coupled monoclonal antibody.

immunolocalization *or* **immunolocalisation** the use of appropriately labelled antibody (or antigen) preparations to detect the position of specific structures or components that contain or are the complementary antigens (or antibodies).

immunological *or (esp. US)* **immunologic** of, concerned with, or pertaining to immunity or immunology. —**immunologically** *adv.*

immunologically competent *(of cells, tissues, etc.)* qualified for and capable of giving an **immune response**.

immunological paralysis *an alternative name for* **acquired tolerance**.

immunological rejection the destruction, by a specific immune reaction, of foreign cells or tissues transplanted or inoculated into a recipient animal from a donor animal.

immunological response any specific response to an antigen. It includes **cell-mediated immunity**, **humoral immunity**, and **immunological tolerance**.

immunological surveillance the postulated monitoring of the cells of large, long-lived animals by their immunological systems so that aberrant cells arising from somatic mutations, and so containing new antigens, are destroyed.

immunological tolerance a type of immunological response in which there develops a specific nonreactivity of the lymphoid tissues towards a given antigen, one that in other circumstances is able to induce cell-mediated or humoral immunity. Immunological tolerance may follow contact with the antigen in fetal or early postnatal life or the administration of the antigen to adults (**acquired tolerance**). The reaction towards other, unrelated antigens is unaffected.

immunology the study of **immunity** and related phenomena. The science of immunology grew out of the study of resistance to infectious disease, and now encompasses the study of antigens, antibodies, and their interactions both *in vivo* and *in vitro*, and the cellular phenomena of recognition of, and responsiveness to, foreign substances. Related disciplines include **immunobiology** and **immunochemistry**.

immunometry the measurement of amounts of substances by the use of specific antigen–antibody reactions. —**immunometric** *adj.*; **immunometrically** *adv.*

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immunomodulation the alteration of an immune response by an agent other than the antigen.

immunomodulator any agent that alters the extent of the immune response to an antigen, by altering the antigenicity of the antigen or by altering in a nonspecific manner the specific reactivity or the nonspecific effector mechanisms of the host. Immunomodulators include adjuvants, immunostimulants, and immunosuppressants.

immunoosmophoresis *an alternative term for* **counter-(immuno)electrophoresis**.

immunophenotyping the **typing** of cells with immunological markers such as monoclonal antibodies.

immunophilin any member of a family of receptors that includes the major **FK506** binding protein **FKBP** and **cyclophilin**. These two proteins are unrelated in amino-acid sequence, but both possess **peptidyl-prolyl isomerase** activity which is blocked by immunosuppressants that block signal-transduction pathways leading to T-cell activation such as FK506 and rapamycin, which block FKBP, or **cyclosporin A**, which blocks cyclophilin. Example, the rapamycin-selective 25 kDa human immunophilin: database code FKB2_HUMAN, 224 amino acids (25.15 kDa).

immunoprecipitate **1** the precipitate formed in an antigen–antibody reaction. **2** to precipitate (something) by reaction with a specific antibody or antigen. —**immunoprecipitation** *n.*

immunoradiometric assay *abbr.*: IRMA; an alternative method to **radioimmunoassay** for the measurement of very small amounts of nonradioactive material. An excess amount of a specific antibody labelled with a radioactive isotope is added to the sample containing the substance to be assayed. After equilibration, unreacted antibody is removed and the amount of radioactive material remaining is measured.

immunoreactive capable of reacting with a specific antibody. The term is used especially of substances that react with an antibody directed against a particular peptide hormone (or part of such a hormone) but that do not necessarily exhibit the expected physiological or pharmacological activity. —**immunoreactivity** *n.*

immunosorbent any sorbent used in, or useful for, **immunosorption**. *See also* **immunoadsorbent**.

immunosorption the use of antigens (or antibodies) immobilized on a solid matrix to remove specifically the complementary antibodies (or antigens) from a mixture and their subsequent elution from the solid phase. It is used in, and is useful for, purification of antibodies (or antigens). *See also* **immunoadsorption**.

immunostimulant any agent that nonspecifically enhances the immunologically specific reactivity of an animal to an antigen and also the animal's nonspecific effector mechanisms. —**immunostimulatory** *adj.*

immunosuppressant *or (sometimes)* **immunosuppressive** any agent that causes **immunosuppression**.

immunosuppressed describing an organism that is incapable of showing an immune response to an antigen.

immunosuppression the suppression of immune responses to antigens. This can be achieved by various means, including physical (e.g. X-irradiation), chemical (e.g. antimetabolic drugs), or biological (e.g. antilymphocyte serum). After transplant surgery **azathioprine** is commonly used. This drug has a preferential effect on T-cell-mediated reactions. It is degraded in the body first to mercatopurine and is then converted to the active agent, the ribotide, which inhibits nucleic-acid synthesis. **Methotrexate**, cyclophosphamide, **cyclosporin A**, and **FK506** are also highly effective immunosuppressants, the latter two being used extensively. Infection by HIV-1 eventually leads to a reduction in the population of helper T-cells and macrophages. This immunosuppression of the system is associated with occurrence of **Kaposi's sarcoma** and allows infection by agents such as *Pneumocystis carini*, cytomegalovirus, and tuberculosis. *Compare* **immunodeficiency**. *See also* **suppressor cell**.

immunosuppressive **1** able to cause **immunosuppression**. **2** *an alternative term for* **immunosuppressant**.

immunosympathectomy the destruction of some or all of the neurons of the sympathetic nervous system by injections into a newborn animal of an antiserum to the appropriate **nerve growth factor**.

immunotoxin any of a class of therapeutic drugs consisting of a monoclonal antibody linked to a toxic protein (e.g. ricin, diphtheria toxin).

IMP *abbr. for* **1** inosine monophosphate; i.e. inosine phosphate. **2** ion-moderated partition.

impaired glucose tolerance *abbr.*: IGT; the term recommended to denote a clinical state or condition of humans that is intermediate between the normal one and the overtly diabetic. Characteristically, in a standard oral **glucose-tolerance test** in non-pregnant adults, the glucose concentration in capillary whole blood or venous plasma taken at 2 hours is in the range 8–11 mmol L^{-1} (1.4–2.0 g L^{-1}); the corresponding values for venous whole blood are 7–10 mmol L^{-1} (1.2–1.8 g L^{-1}). In addition, the fasting plasma glucose must be below 8 mmol L^{-1}, and plasma glucose during the test must be greater than 11 mmol L^{-1} at 30, 60, and 90 min.

IMP cyclohydrolase EC 3.5.4.10; *other names*: IMP synthetase; inosinicase; an enzyme of the pathway for *de novo* purine biosynthesis that cyclizes 5-formamido-1-(5′-phosphoribosyl)imidazole-4-carboxamide to IMP with elimination of H_2O. For an example, *see* **phosphoribosylaminoimidazolecarboxamide formyltransferase**.

IMP dehydrogenase EC 1.1.1.205; *other name*: inosine-5′-monophosphate dehydrogenase; an enzyme that catalyses the conversion of inosine 5′-phosphate, NAD^+, and H_2O to xanthosine 5′-phosphate and NADH. The reaction involves the introduction of an oxo group at the purine C-2. Xanthosine 5′-phosphate is then converted to guanosine 5′-phosphate by **GMP synthase** (glutamine hydrolysing). Examples from human, in which there are two isoenzymes: database code IMP1_HUMAN, 514 amino acids (55.39 kDa); database code IMP2_HUMAN, 514 amino acids (55.74 kDa).

impedance *symbol*: Z; the quality determining the amplitude of the current flowing in a circuit for a given applied alternating electric potential. It depends upon the electric resistance, self-inductance, and capacitance of the circuit.

impeller **1** the vaned, rotating disk of a centrifugal pump. **2** any device incorporating an **impeller** (def. 1).

impermeable (of a substance or structure) not permitting the passage through it of a fluid or of a particular solute in a fluid; not permeable. —**impermeability** *n.*

impermeant (of a fluid or a solute in a fluid) incapable of passing through a particular substance or structure.

imprinting *(in genetics)* the differential degree to which the effects of maternally and paternally derived DNA are exerted. For example, the onset of Huntington's disease is earlier if the defective allele is inherited from the father rather than the mother.

impulse **1** *(in physics)* a vector quantity equal to the integral of the force, F, acting on a body with respect to the time, t, over which the force acts: $\int F dt$. If the force is constant the expression reduces to the product Ft. It also equals the total change of momentum of the body induced by the applied force. **2** *(in physics)* an electrical surge of unidirectional polarity. **3** *(in physiology) or* **nerve impulse** an all-or-none signal propagated along the axons of neurons by which information is transmitted rapidly and precisely through the nervous system. It consists of a sequence of changes in ionic permeability of the neuronal membrane that gives rise to ionic currents and associated changes in transmembrane electrical potential.

impure not pure, lacking purity; (of a substance or material) containing contaminants.

impurity **1** the state or quality of being impure. **2** any or all of the admixed components in an impure substance or material.

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impurity quenching **chemical quenching** due to an **impurity** (def. 2).

In *symbol for* indium.

inappropriate secretion a clinical syndrome in which the secretion of a specified hormone, commonly **antidiuretic hormone**, is abnormally high relative to the state of the normal regulatory mechanisms. It is so termed because it results from an unknown or unmistakably abnormal cause and serves no recognizable homeostatic function.

inborn error of metabolism any of the genetically determined biochemical variations occurring in humans. They are highly specific and represent many diverse metabolic phenomena, resulting in very varied effects on the viability of the individual.

inbred strain *or* **inbred line** a group of organisms obtained by repeated inbreeding over several successive generations, e.g. by self-pollination in plants or by repeated brother × sister matings in animals. Eventually, all individuals will possess identical sets of **autosomes**, and all the chromosome pairs will become homozygous.

inclusion *(in cytology)* **1** any discrete body or particle within a cell, especially a passive product of cell activity such as a starch or volutin granule. **2** *an alternative (less common) name for* **inclusion body**.

inclusion body *or* **inclusion** **1** any discrete assembly of virions and/or viral particles that may be visualized in virus-infected cells, either in the nucleus or in the cytoplasm. **2** *(in bacteriology)* any one of a number of bodies found within bacterial cells, e.g. storage granules, gas vacuoles, carboxysomes.

inclusion cell *abbr.*: I cell; a type of cell that is seen in tissues from patients with mucolipidosis II **(I-cell disease)** and that contains inclusions consisting of very large lysosomes whose contents are heterogeneous, comprising mucopolysaccharide, whorls of membrane, and other material.

inclusion-cell disease *or* **mucolipidosis II** *see* **I-cell disease**.

inclusion complex *or* **inclusion compound** any chemical complex in which one component (the host molecule) forms a crystal lattice containing tunnel- or channel-shaped spaces in which molecular entities of a second species (the guest molecule) are located. There is no bonding between the host and the guest molecules.

incompatibility **1** a criterion for classifying bacterial **plasmids**; two plasmids of the same incompatibility group cannot coexist in one host cell. The molecular basis is that the incompatible plasmids share sites during plasmid **segregation** (def. 3). **2** the state of being **incompatible**.

incompatibility group a group to which plasmids are said to belong if they cannot coexist in the same bacterial host over several generations without selection.

incompatible **1** *(in immunology)* having antigenic nonidentity between a donor and a recipient, e.g. in blood transfusion or tissue transplantation. **2** *(in therapeutics) (of two drugs)* incapable of being used together or combined; antagonistic.

incomplete antibody **1** any antibody whose activity in an agglutination test can only be demonstrated indirectly, e.g. by an antiglobulin test. **2** *(sometimes)* a univalent antibody fragment produced enzymically, e.g. a **Fab fragment**.

incomplete Freund's adjuvant *see* **Freund's adjuvant**.

incorporation **1** the act or process of including (something) as a part of a whole. **2** *(in biochemistry)* the inclusion of (isotopically labelled) metabolites, by covalent linkage, into biopolymers by living cells or cell-free preparations; often taken as an index of biosynthesis. —**incorporate** *vb.*

incretin a putative insulinogenic principle secreted from the duodenum and jejunum in response to the presence of glucose. Its effects are now generally considered to be attributable to **glucose-dependent insulinotropic peptide**.

incubate **1** to maintain at an appropriate temperature so as to favour growth, development, or continued survival (e.g. of cells); by extension, to maintain under specified conditions in a controlled or artificial environment (e.g. in studies of enzymic or antigen–antibody reactions), especially at a particular ambient temperature (which may be above or below that of the environment). **2** a material or preparation that has been incubated. —**incubation** *n.*

incubation mixture any reaction mixture that is maintained at a controlled temperature and/or in a controlled, artificial environment.

incubation period **1** *(in pathology)* the time interval between the invasion of an organism by a pathogenic virus or microorganism and the overt manifestation of disease. **2** *(in microbiology)* the period of development of a culture of bacteria or other microorganisms.

incubator any closable, heat-insulated cabinet that is maintained at a constant internal temperature (and, sometimes, humidity and/or atmosphere) and that is used for the growth or maintenance of cells, cultures, tissues, or organisms, or for the hatching of eggs.

Inderal *see* **propranolol**.

index of refraction *see* **refractive index**.

Indian tobacco *see* **lobelia**.

indican **1 metabolic indican** indol-3-yl hydrogensulfate; 3-indoxylsulfuric acid; a so-called ethereal sulfate, formed in the gut by bacterial action on tryptophan and excreted in the urine, where its level may be taken as an index of intestinal stagnation. **2 plant indican** indol-3-yl-β-D-glucopyranoside; indoxyl-β-D-glucoside; a substance isolated from *Indigofera* spp., members of the Leguminosae, and *Polygonium tinctorium*. The glucoside is hydrolysed during extraction by water or dilute acid, and the indoxyl is liberated spontaneously, oxidizing to the blue dye indigo.

indicated hydrogen *symbol: H- (or sometimes H)* (with a prefixed locant); *(in chemical nomenclature)* an atom of hydrogen whose position in the molecular structure of an unsaturated cyclic organic compound or group requires to be explicitly stated in order to make the name of the compound or group specific to a particular structural isomer (or tautomer) if otherwise the name would apply equally to two or more isomers (or tautomers). The compound or group in question commonly consists of or is derived from a condensed ring system with the maximum number of non-cumulative double bonds, although the notation is applied also to certain monocyclic systems. The symbol (with its locant) ordinarily precedes the name or the relevant part of the name, e.g. 1*H*-purin-6-amine or 6-amino-1*H*-purine (alternative semisystematic names for one of the tautomers of adenine); however, where the insertion of a substituent into a cyclic structure has necessitated the addition of a hydrogen atom at another position the symbol is placed in parentheses after the locant for the substituent, e.g. purin-6(1*H*)-one (*a semisystematic name for* one of the tautomers of hypoxanthine).

indicator **1** any substance used in a chemical operation to indicate by a colour change the completion of a reaction or the attainment of a desired state. **2** any substance that by a characteristic colour change indicates the presence of another particular substance. **3** (*in* **saturation analysis**) the labelled substance whose distribution between the reactants of the system is used to determine the amount of analyte present. **4** an isotope, often a radioactive one, that is used as a tracer.

indicator enzyme *an alternative name for* **marker enzyme**.

indicator organism *or* **indicator species** any species of organism whose presence or population characteristics in a particular habitat are used to provide information about the nature of that habitat, especially regarding its degree of pollution.

indicator yellow *the original name for N*-retinylidene opsin. It was so called because its colour changes between yellow and orange according to the pH of its aqueous solution. It spontaneously hydrolyses into opsin and (all-*trans*-)retinal. *See* **rhodopsin**.

indigo a blue dye prepared from the same plants as plant **indican**. Its major blue component is **indigotin**.

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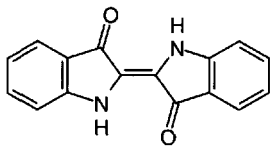
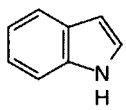
indigotin [$\Delta^{2,2'}$-biindoline]-3,3′-dione; the major blue component of **indigo**.



indirect antagonism a form of **antagonism** (def. 2) arising as a consequence of competition by the antagonist for the binding site of an intermediate that links receptor activation to the observed effect.

INDO-1 1-[2-amino-5-(6-carboxyindol-2-yl)phenoxy-2-(2-amino-5-methylphenoxy)ethane-*N*,*N*,*N*′,*N*′-tetraacetic acid; a fluorescent calcium chelator, named from the indolyl moiety, that can be used as an indicator of Ca^{2+} concentration; it has a large shift in fluorescence emission, from 480 to 400 nm, on binding Ca^{2+}.

indole 2,3-benzopyrrole; a compound formed by the degradation of tryptophan.



indoleacetate *abbr.*: IAA; the anion of indole-3-acetic acid. Formed from L-tryptophan, it is a plant hormone, and the main **auxin** of higher plants.

indoleacetonitrile *abbr.*: IAN; an **auxin**, second in abundance to indoleacetate.

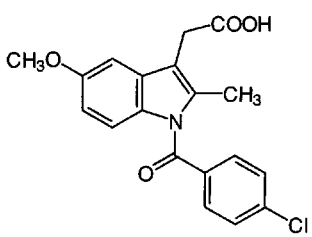
indole-3-glycerol-phosphate synthase *see* ***trp* genes**.

indole test a test used for the identification of certain microorganisms, e.g. members of the Enterobacteriaceae. It determines the ability of the organism to produce indole from tryptophan.

indolicidin a bactericidal and fungicidal 13-residue peptide amide from the cytoplasmic granules of bovine neutrophils. It contains five tryptophan residues, hence its name. Some therapeutic success has been achieved in animals against the fungus, *Aspergillus fumigatus*, using liposomally encapsulated indolicidin, indicating that neutrophil-derived antimicrobial peptides may have therapeutic value.

indoluria the presence in (human) urine of compounds containing an indole ring.

indomethacin 1-(*p*-chlorobenzoyl)-5-methoxy-2-methylindole-3-acetic acid; an inhibitor of **prostaglandin-endoperoxide synthase**. It is useful as an anti-inflammatory drug.



INDOR *abbr. for* internuclear double resonance spectrometry.

induced enzyme *or* **inducible enzyme** any enzyme that is synthesized in a cell only in very small amounts except when induced by the presence of its substrate or a closely related compound. *Compare* **constitutive enzyme**.

induced-fit theory a possible explanation, first proposed by D. E. **Koshland**, of enzyme specificity. It suggests that reaction between an enzyme and its substrate can occur only following a change in the enzyme's structure, induced by the substrate itself. It is proposed that: (1) a precise orientation of catalytic groups is required for enzyme action; (2) the substrate may cause an appreciable change in the three-dimensional relationship of the amino-acid residues at the active site; and (3) the changes in enzyme structure caused by a substrate will bring the catalytic groups into the proper orientation for reaction, whereas a nonsubstrate will not. It is similar to the **zipper model** of hormone–receptor interaction. *Compare* **lock-and-key model**.

inducer any compound that causes cells to produce larger amounts of the particular enzymes involved in its uptake and/or metabolism (or in the uptake and/or metabolism of a structurally similar compound), than are found in cells when the inducer is absent.

inducible capable of being induced.

inducible enzyme *an alternative name for* **induced enzyme**.

induction **1** *see* **Jacob–Monod model**. **2** *(in physics)* any physical effect brought about (i.e. induced) in an object by the action of a field without any direct physical contact with the inducer. It may be electrostatic, magnetic, or electromagnetic. *See also* **induced enzyme**.

induction coil a device for producing a rapid succession of large pulses of induced emf in a secondary coil from an intermittent low emf in a primary coil.

induction motor an electric motor in which an alternating current is supplied to the winding of the stator, arranged in such a manner as to produce in effect a rotating magnetic field. This in turn induces electric currents in the winding of the rotor, and interaction between these currents and the magnetic flux exerts a torque on the rotor. Induction motors are useful in situations where sparks caused by moving electric contacts are undesirable.

inductive effect *(in chemistry) symbol*: *I*; an experimentally observable effect (on reaction rates, etc.) caused by the transmission of charge through a chain of atoms by electrostatic induction. It is symbolized by $+I$ or $-I$, according to whether the group in question is left with a small positive or a small negative charge.

+ine *suffix* designating **1** an organic compound that is either an amine (including any monoamino monocarboxylic acid other than tryptophan), or a nitrogen-containing heterocycle other than one containing four or five atoms in the ring. **2** a halogen. **3** any of a group of certain inorganic binary hydrogen compounds, namely arsine, bismuthine, phosphine, and stibine; also hydrazine.

inert **1** having little or no ability to react chemically or physiologically. **2** having no inherent ability to move or resist being moved. **—inertness** *n.*

inertia **1** *(in physics)* the tendency of an object to resist changes to its state of rest or uniform motion; by analogy extended to other physical qualities that resist change. **2** the state of being inert or inactive. **—inertial** *adj.*

inertial mass *see* **mass**.

infect **1** to cause infection in (an organism, wound, etc.), especially with pathogenic microorganisms. **2** to affect or become affected with a communicable disease.

infection **1** the invasion of a cell or organism by other (especially pathogenic) organisms. **2** the act or process of infecting; the state of being infected. **3** any agent or process that infects.

infectious **1** *(of a disease)* caused by pathogenic (micro)organisms. **2** causing or transmitting infection. **3** *(of a disease)* capable of being transmitted to another organism. **—infectiously** *adv.*; **infectiousness** *n.*

infectious mononucleosis *see* **Epstein–Barr virus**.

infectious viral nucleic acid a purified viral nucleic acid that, when it infects a host cell, causes the production of progeny viral particles.

infective **1** capable of causing infection. **2** *an alternative (less*

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common) word for **infectious**. —**infectively** *adv.*; **infectiveness** *or* **infectivity** *n.*

infinite having no limits in extent, magnitude, space, or time; immeasurably numerous or great. —**infiniteness** *n.*; **infinitely** *adv.*

infinite dilution a hypothetical state (of a solution) in which the solute concentration is considered to be zero and the activity coefficient unity.

infinitely thick *(of a radioactive sample)* having a thickness no less than **infinite thickness** for the particular radionuclide to be measured.

infinitely thin *(of a radioactive sample)* having a thickness no greater than **infinite thinness** for the particular radionuclide to be measured.

infinite thickness the thickness of a sample containing a particular radionuclide, especially a soft beta-emitter, beyond which, because of self-absorption, any increase results in no further increase in recordable disintegrations. Under these conditions the (radio)activity is proportional to the specific (radio)activity of the substance.

infinite thinness the thickness of a sample containing a particular radionuclide at or below which self-absorption is negligible. Under these conditions the (radio)activity is proportional to the amount of the radionuclide present.

inflammable very liable to catch fire and produce flame; flammable.

inflammation the immediate defensive reaction of vertebrate tissue to infection or to injury by chemical or physical agents. The part affected is characterized by pain, heat, redness, swelling, and loss of function; there is local vasodilatation, extravasation of plasma into the intercellular spaces, and accumulation of white blood cells and other macrophages in the injured part. Plasma enzyme systems are important sources of inflammatory mediators. These include the **complement**, **blood coagulation**, fibrinolytic, and **kinin** systems. Also active are the mediators released by mast cells, basophils, and platelets, as well as the eicosanoids generated by many cells at inflammatory sites. —**inflame** *vb.*

informatics the science concerned with the structure and properties of scientific information, its theory, history, methodology, and organization. *Compare* **information science**. —**informatical** *adj.*; **informatician** *n.*

informatin *see* **informofer**.

information **1** communicated or communicable factual knowledge; data; news. **2** **genetic information**. **3** *(in computing)* the results obtained by processing raw data according to programmed instructions.

informational **1** of, pertaining to, giving, or carrying information. **2** *(in biochemistry)* describing any biological macromolecule that contains or transmits **genetic information** in the form of specific sequences of nucleotides or amino acids.

information retrieval the selective tracing and recovery of information stored in printed works, computers, etc.

information science the science concerned with the procedures by which information, especially scientific or technical information, is stored, retrieved, and disseminated. *Compare* **informatics**.

information theory the quantitative theory of the coding and transmission of signals and information.

informofer a specific, 30S macroglobular particle consisting of the protein **informatin**. Informofers are present in the cell nucleus, tightly packed along molecules of **heterogeneous nuclear RNA**.

informosome a cytoplasmic mRNA-carrying ribonucleoprotein particle of relatively low buoyant density. Informosomes are believed to function in the protection of mRNA from nuclease attack and in the transport of mRNA from the nucleus to the cytoplasm.

infra+ *prefix* denoting below, beneath, coming after, within. *Compare* **sub+**, **supra+**, **ultra+** (def. 1).

infradian describing any biological activity that occurs, or varies cyclically, more often than once every 24 hours. *Compare* **circadian**, **ultradian**.

infranatant **1** lying below. **2** a solid or liquid lying below a **supernatant** liquid. *Compare* **subnatant**.

infrared of, pertaining to, or being **infrared radiation**.

infrared dichroism the **dichroism** of polarized infrared radiation. It is used in studies of polypeptide structure.

infrared radiation *abbr.*: IR *or* i.r.; electromagnetic radiation of wavelengths in the range 730 nm to 1 mm (frequencies 300 GHz to 410 THz). This range lies between those of visible light and microwaves.

infrared spectrophotometer any instrument for **infrared spectrophotometry**.

infrared spectrophotometry the measurement of the absorption or emission of infrared radiation at particular wavelengths or frequencies. *See* **infrared spectrum**.

infrared spectrum any absorption spectrum or emission spectrum of infrared radiation. It includes photons that are absorbed or emitted during vibrational and rotational transitions in a molecule. Infrared spectra are widely used in organic chemistry to identify particular groups of atoms by their characteristic vibrational frequencies.

infuse **1** to introduce gradually, as of a solution into a vein or body cavity. **2** to make an **infusion** (def. 2).

infusion **1** the process of infusing. **2** an extract, e.g. of meat or leaves, obtained by soaking in water.

ingest to take material, e.g. food or liquid, into a cell or organism. —**ingestible** *adj.*; **ingestion** *n.*; **ingestive** *adj.*

inhibin one of several polypeptides (another is **activin** of the transforming growth factor β family) that participate in differentiation and growth of diverse cell types. Inhibin and activin are glycoproteins, secreted by the gonads. Inhibin inhibits secretion of **follicle-stimulating hormone** by the pituitary. It is present in seminal plasma and follicular fluid. It has an M_r of 31 000, and consists of two subunits crosslinked by disulfide bridges. There are two isoforms, A and B, with the same α subunit but different β subunits. Inhibin A is a dimer of α and β_A subunits, and inhibin B is a dimer of α and β_B subunits. Example of the α chain, from *Mus musculus*: database code IHA_MOUSE, 366 amino acids (39.54 kDa). The inhibin/activin precursor is a protein generated by alternative splicing of a gene for subunits for both activin and inhibin. Examples of β chains, inhibin β_A chain (precursor) from human (*other name*: erythroid differentiation protein; *abbr.*: EDF): database code IHBA_HUMAN, 426 amino acids (47.39 kDa); amino acids 311–426 are the inhibin β_A chain; inhibin β_B chain (precursor) from *Bos taurus*: database code IHBB_BOVIN, 408 amino acids (44.89 kDa).

inhibit **1** to restrain or hinder. **2** to stop, prevent, or reduce the rate of (some process, e.g. the growth or functioning of an organism or part of an organism, or a chemical or enzymic reaction).

inhibition constant *symbol*: K_i; the equilibrium (dissociation) constant for the reaction: $EI \rightleftharpoons E + I$. It is given by $K_i = [E][I]/[EI]$, where E is the enzyme and I the inhibitor, the square brackets indicating concentrations.

inhibition index an inverse measure of the potency of an antimetabolite. It is the ratio of the concentration of antimetabolite that is required to inhibit the biological effect of unit concentration of corresponding metabolite.

inhibitor **1** any agent that inhibits. **2** *(in biochemistry)* any substance that inhibits an enzymic reaction. *See also* **competitive inhibition**, **noncompetitive inhibition**, **uncompetitive inhibition**.

initial velocity *or* **initial steady-state rate** *symbol*: v_o *or* v; the reaction velocity in the earliest stage of an enzyme-catalysed reaction. It is given by the tangent at the origin to the curve of reaction velocity as a function of time. In practice it is often measured over the period when the initial substrate concentration has diminished by <5%.

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initiation 1 the formation of **initiation complex(es)** at the start of ribosome-mediated translation of mRNA into polypeptide. 2 the first stage in carcinogenesis, in which a normal cell is converted to a precancerous one. 3 the first step in a chain reaction. —**initiate** *vb.*; **initiatory** *adj.*

initiation codon *or* **initiator codon** the codon AUG (or, sometimes in prokaryotes, GUG) that binds *N*-formylmethionyl-$tRNA_f^{Met}$ in prokaryotes or initiator methionyl-$tRNA_f^{Met}$ in eukaryotes, and serves as a signal for the start of polypeptide synthesis at the ribosome.

initiation complex any of the complexes formed at the start of ribosome-mediated translation of mRNA into polypeptide. They contain mRNA, initiation factors, initiator fMet-$tRNA_f$ or Met-$tRNA_f^{Met}$, one or two ribosomal subunits, and sometimes GTP. *See* **initiation factor**.

initiation factor *abbr.*: IF (in prokaryotes) *or* eIF (in eukaryotes); any of a group of soluble proteins that function in the initiation of ribosome-mediated translation of mRNA into polypeptide. Among prokaryotic initiation factors, those of *Escherichia coli* are well characterized. This organism has three principal initiation factors, each consisting of a single polypeptide chain. **IF-1** is a basic, stable protein of M_r 9000. It is a stimulator of IF-2 and IF-3. Example: database code IF1_ECOLI, 71 amino acids (8.11 kDa). There are two forms of **IF-2**: IF-2a, which is acidic, unstable, and of M_r 115 000 and the almost equally active artefactual product, IF-2b, formed by limited proteolysis of IF-2a. It is a GTP-binding protein, protects formylmethionyl-$tRNA_f^{Met}$ from spontaneous hydrolysis, and promotes its binding to the 30S ribosomal subunits; it is also involved in the hydrolysis of GTP during the formation of the 70S ribosomal complex. By using alternative initiation codons in the same reading frame, the gene is translated to give three isozymes, α (example), β, and β′, having different N termini. Example: database code IF2_ECOLI, 894 amino acids (97.74 kDa). **IF-3** is a basic, stable protein of M_r 22 000. It binds to the 30S ribosomal subunit and shifts the equilibrium between 70S ribosomes and their subunits in favour of the free subunits, thus enhancing the availability of 30S subunits on which protein synthesis initiation begins. It is also a translational repressor of its own gene. Example: database code IF3_ECOLI, 180 amino acids (20.54 kDa). IF-1, IF-2, and IF-3 bind cooperatively to a 30S ribosomal subunit to form a 30S·IF-1·IF-2·IF-3 particle in which the three initiation factors are bound contiguously near the 3′ end of 16S RNA in a 30S ribosomal subunit. This particle subsequently binds mRNA at a site that includes the initiation codon AUG (or GUG), initiator fMet-$tRNA_f^{Met}$, and GTP with concomitant release of IF-3 to form a 30S initiation complex, 30S·IF-1·IF-2·mRNA·GTP·fMet-$tRNA_f^{Met}$. Joining of a 50S ribosomal subunit with concomitant release of IF-1, IF-2, GDP, and P_i forms a 70S initiation complex, mRNA·70S·fMet-$tRNA_f^{Met}$.

In eukaryotes there are more initiation factors and many have been characterized in lysates of rabbit reticulocytes, they include: eIF-1 (single polypeptide chain, M_r 15 000); eIF-2 (three nonidentical polypeptide chains, M_r 150 000); eIF-3 (nine nonidentical polypeptide chains, M_r 700 000); eIF-4A (single chain, M_r 49 000); eIF-4B (single chain, M_r 80 000); eIF-4C (single chain, M_r 17 500); eIF-4D (single chain, M_r 16 500); eIF-5 (single chain, M_r 190 000); Co.eIF-2 (single chain, M_r 22 000); cap-binding protein (single chain, M_r 24 000). eIF-2, initiator Met-$tRNA_f^{Met}$, and GTP form a ternary complex; eIF-3 promotes ribosomal dissociation and stabilizes binding of ternary complex to a 40S ribosomal subunit to form the complex 40S·eIF-2·eIF-3·Met-$tRNA_f^{Met}$·GTP. Then eIF-1, eIF-4A, eIF-4B, eIF-4C, and cap-binding protein promote binding of mRNA and ATP-dependent formation of a **40S initiation complex**, 40S·eIF-2·eIF-3·Met-$tRNA_f^{Met}$·mRNA. Factor eIF-5 is required for formation of an **80S initiation complex**, 80S·Met-$tRNA_f^{Met}$·mRNA, from a 40S complex, together with hydrolysis of the bound GTP and release of initiation factors. Co.eIF-2 stimulates ternary complex formation.

initiation signal 1 any of the purine-rich regions of mRNA on the 5′ side of the initiation codon that serve to distinguish the latter from other similar codons. 2 any of the promoter regions of DNA on the 5′ side of the start of transcription to form mRNA.

initiator 1 a gene product that interacts specifically with the replicator site on a replicon resulting in the initiation of a new round of DNA replication. 2 a starting point for either nucleic-acid transcription or translation. 3 a carcinogen that initiates the first stage of carcinogenesis. 4 any compound that, when added to monomer, initiates a polymerization reaction.

initiator codon *see* **initiation codon**.

initiator transfer RNA *abbr.*: $tRNA_f^{Met}$; any of the tRNA molecules that, when aminoacylated, specifically binds to an initiation codon (usually AUG) in mRNA at the start of ribosome-mediated translation of mRNA into polypeptide. In prokaryotes it is *N*-formylmethionyl-$tRNA_f^{Met}$, and in eukaryotes it is methionyl-$tRNA_f^{Met}$; neither is able to promote the insertion of methionine residues at internal sites.

innate being an essential characteristic of an organism or thing; inborn.

innervation the nerve supply to an organ or part.

Ino *symbol for* a residue of the ribonucleoside inosine (alternative to I).

inoculate 1 to introduce cells, microorganisms, or viruses into or onto a culture medium. 2 to introduce causative agents of disease (alive, dead, or attenuated) into an animal or person for the purpose of immunization. —**inoculation, inoculator** *n.*; **inoculative** *adj.*

inoculum (*pl.* **inocula**) a quantity or suspension of cells, microorganisms, or viruses used to start a new culture or to infect another culture; something used to inoculate.

Ino-3′,5′-*P* *symbol for* inosine 3′,5′-phosphate.

Ino5′*P* *symbol for* inosine 5′-phosphate.

Ino5′*PP* *symbol for* inosine 5′-diphosphate (alternative to ppI).

Ino5′*PPP* *symbol for* inosine 5′-triphosphate (alternative to pppI).

inorganic not having the characteristics of living organisms; not **organic**.

inorganic biochemistry the branch of biochemistry concerned with the role of inorganic substances in biochemical systems. *Compare* **bioinorganic chemistry**.

inorganic chemistry the branch of chemistry dealing with the elements and all their compounds other than ones containing carbon, except for carbon itself and some simple compounds of carbon, e.g. oxides, sulfides, and cyanides.

inorganic diphosphate *symbol*: PP_i; any of the anions formed from diphosphoric acid, $(HO)_2PO–O–PO(OH)_2$, or any mixture of the acid and its anions. The older term **inorganic pyrophosphate** may be retained but is now less preferable.

inorganic phosphate *or* **inorganic orthophosphate** *symbol*: P_i; any of the anions formed from [ortho]phosphoric acid, $PO(OH)_3$, or any mixture of the acid and its anions.

inorganic pyrophosphatase an enzyme, EC 3.6.1.1, often less precisely termed pyrophosphatase; *systematic name*: pyrophosphate phosphohydrolase. It catalyses the hydrolysis of pyrophosphate by two molecules of orthophosphate. Example from *Escherichia coli*: database code IPYR_ECOLI, 175 amino acids (19.55 kDa).

inorganic pyrophosphate *another (less preferred) term for* **inorganic diphosphate**.

iNOS *see* **nitric-oxide synthase**.

inosinate 1 either the mono- and/or the di-anion of **inosinic acid**. 2 any mixture of the acid and its anions. 3 any salt or ester of inosinic acid.

inosine *symbol*: I *or* Ino; hypoxanthosine; hypoxanthine riboside; 9-β-D-ribofuranosylhypoxanthine; a nucleoside found free, especially in meat, sugar beet, and yeast, but not in combination in nucleic acids except in the anticodons of some

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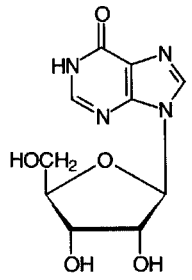
transfer RNAs. It may be formed by the action of adenosine deaminase (EC 3.5.4.4) in the first step of the breakdown of adenosine to uric acid, and it occurs as an intermediate in the recycling of both adenosine and inosine 5′-phosphate by **salvage pathways**.



inosine 3′,5′-(cyclic)phosphate *or* **inosine 3′,5′-cyclophosphate** *see* **inosine 3′,5′-phosphate**.

inosine 5′-diphosphate *symbol*: Ino5′*PP or* ppI; *recommended name for* inosine diphosphate (*abbr.*: IDP), 5′-diphosphoinosine, 5′-inosinyl phosphate, inosine 5′-(trihydrogen diphosphate). It is an intermediate in the formation of inosine 5′-triphosphate from inosine 5′-phosphate.

inosine monophosphate *abbr.*: IMP; *an alternative name for* any **inosine phosphate**, but particularly for **inosine 5′-phosphate**, especially when its distinction from inosine (5′-)diphosphate and inosine (5′-)triphosphate requires emphasis.

inosine-5′-monophosphate dehydrogenase *see* **IMP dehydrogenase**.

inosine phosphate inosine monophosphate (*abbr.*: IMP); any phosphoric monoester or diester of inosine. Of the three possible monoesters – the 2′-phosphate, the 3′-phosphate, and the 5′-phosphate – only **inosine 5′-phosphate** is of any importance (the locant being omitted if no ambiguity may arise). The only diester of significance is **inosine 3′,5′-phosphate**.

inosine 3′,5′-phosphate *symbol*: Ino-3′,5′-*P*; *the recommended name for* cyclic inosine 3′,5′-monophosphate (*abbr.*: 3′,5′-cyclic IMP *or* cyclic IMP *or* cIMP), inosine 3′,5′-cyclophosphate, inosine 3′,5′-(cyclic)phosphate; a monophosphoric diester of inosine. It is a cyclic nucleotide similar in structure and metabolism to **adenosine 3′,5′-phosphate** (i.e. cyclic AMP) but only rarely encountered.

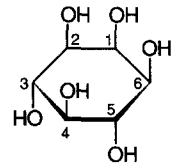
inosine 5′-phosphate *or* **5′-inosinic acid** *or* **5′-phosphoinosine** *or* **5′-*O*-phosphonoinosine** *symbol*: Ino5′*P*; *alternative recommended names for* inosine monosphosphate (*abbr.*: IMP), inosine 5′-(dihydrogen phosphate), hypoxanthine ribonucleotide. (The locant is commonly omitted if there is no ambiguity as to the position of phosphorylation.) It is the initial biosynthetic product containing an intact purine nucleus, its immediate precursor being 4-carbamoyl-5-formamidoimidazole riboside 5′-phosphate. Hence IMP is a key intermediate in the biosynthesis of all other purine nucleotides and in the formation of purine nucleosides and free purines. In addition, resynthesis of IMP from hypoxanthine can be effected via a **salvage pathway** by the action of hypoxanthine phosphoribosyltransferase (EC 2.4.2.8) (*see* **phosphoribosyltransferase**).

inosine 5′-triphosphate *symbol*: Ino5′*PPP or* pppI; *the recommended name for* inosine triphosphate (*abbr.*: ITP), 5′-triphosphoinosine, 5′-inosinyl diphosphate, inosine 5′-(tetrahydrogen triphosphate). ITP can substitute for adenosine 5′-triphosphate or guanosine 5′-triphosphate in certain enzymic reactions. It is formed from inosine 5′-diphosphate by transfer of the terminal phosphoric residue from adenosine 5′-triphosphate through the action of nucleoside-diphosphate kinase (EC 2.7.4.6).

inosinic acid *the trivial name for* any phosphoric monoester of inosine. The position of the phosphoric residue on the ribose moiety of a given ester may be specified by a prefixed locant (*see* **inosine phosphate**). However, 5′-inosinic acid is the ester commonly denoted, its locant usually being omitted if no ambiguity may arise. 5′-Inosinic acid is also an alternative recommended name for **inosine 5′-phosphate**.

inosinyl the inosine [mono]phospho group; the acyl group derived from **inosinic acid**.

inositol **1** *symbol*: Ins; *the common name for* the cyclitol ***myo*-inositol** (*formerly called meso*-inositol *or i*-inositol *or* bios I *or* muscle sugar); 1,2,3,5/4,6-cyclohexanehexol; a growth factor for animals and microorganisms, widely distributed in nature. Inositol occurs free, as various phosphates, or as a constituent of certain phospholipids (*see* **phosphatidylinositol**); in plants it also occurs as its hexaphosphate phytate. Note: whereas *myo*-inositol itself is achiral, its phosphorylated derivatives are chiral and the numbering of their carbon atoms can be confusing. For a proposed solution of the problem, *see* **Agranoff's turtle**. **2** *generic name for* any member of a subclass of cyclitols comprising the nine possible 1,2,3,4,5,6-cycloxanehexols, of which inositol (def. 1) is the most prevalent and most important.



inositol-1,4-bisphosphate 1-phosphatase EC 3.1.3.57; *systematic name*: D-*myo*-inositol-1,4-bisphosphate 1-phosphohydrolase; *other name*: inositol polyphosphate 1-phosphatase; an enzyme involved in the degradation of inositol phosphates that hydrolyses D-*myo*-inositol 1,4-bisphosphate to D-*myo*-inositol 4-phosphate and orthophosphate. Example (bovine): database code INPP_BOVIN, 400 amino acids (43.88 kDa).

inositol phosphate any phosphoric ester of an inositol, but normally referring to the esters of *myo*-inositol (*abbr.*: Ins). Of particular interest are those formed as a result of the hydrolysis of membrane phosphoinositides following activation of phosphoinositide-specific phospholipase C (*see* **phospholipase**). The abbreviation Ins is reserved for *myo*-inositol, and the generalized abbreviation for phosphorylated *myo*-inositols follows the convention Ins(numbers of the carbons bearing phosphorylated hydroxyls)P_x, where P_x indicates the number of phosphates. They include inositol 1,4,5-trisphosphate (*abbr.*: Ins(1,4,5)P_3), formed by phospholipase C action on phosphatidylinositol 4,5-bisphosphate. Ins(1,4,5)P_3 has a number of physiological actions related to the **phosphatidylinositol cycle**. It can be phosphorylated to Ins(1,3,4,5)P_4, which is also physiologically active in calcium metabolism. Other inositol phosphates are intermediates in the degradation of Ins(1,4,5)P_3 and Ins(1,3,4,5)P_4. Ins(1,4,5)P_3 is hydrolysed to Ins(1,4)P_2, which is hydrolysed to Ins(4)*P* and thence to Ins. Ins(1,3,4,5)P_4 is hydrolysed to Ins(1,3,4)P_3 which is hydrolysed to either Ins(1,3)P_2 or Ins(3,4)P_2 these being hydrolysed to Ins(1)*P* or Ins(3)*P* respectively and thence to Ins.

inositol-1,3-bisphosphate 3-phosphatase EC 3.1.3.65; an enzyme that hydrolyses D-*myo*-inositol 1,3-bisphosphate to D-*myo*-inositol 1-monophosphate and orthophosphate.

inositol-1,3,4,5-tetrakisphosphate 3-phosphatase EC 3.1.3.62; an enzyme that hydrolyses D-*myo*-inositol 1,3,4,5-tetrakisphosphate to D-*myo*-inositol 1,4,5-trisphosphate and orthophosphate.

inositol-1,4,5-trisphosphate 1-phosphatase EC 3.1.3.61; an enzyme that hydrolyses D-*myo*-inositol 1,4,5-trisphosphate to D-*myo*-inositol 4,5-bisphosphate and orthophosphate.

inositol-1,4,5-trisphosphate 5-phosphatase EC 3.1.3.56; *systematic name*: D-*myo*-inositol-1,4,5-trisphosphate 5-phos-

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phohydrolase; *other names*: inositol trisphosphate phosphomonoesterase; inositol polyphosphate 5-phosphatase; 5PTase; an enzyme that hydrolyses D-*myo*-inositol 1,4,5-trisphosphate to D-*myo*-inositol 1,4-bisphosphate and orthophosphate. The enzyme has two types, I and II, with different activities; type I (but not type II) hydrolyses inositol 1,3,4,5-tetrakisphosphate to inositol 1,3,4-trisphosphate; neither enzyme acts on the latter or on inositol 1,4-bisphosphate. Example (precursor, fragment) from human: database code IT5P_HUMAN, 672 amino acids (76.96 kDa).

inosyl any chemical group formed by the loss of a 2′-, 3′-, or 5′-hydroxyl group from the ribose moiety of **inosine**.

inotropic influencing contractility of muscles, especially cardiac muscle.

Ins *symbol for* a residue of the cyclitol 1-D-*myo*-inositol (*see* **inositol** (def. 1)).

insect any small air-breathing arthropod of the class Insecta, typically having a segmented body with an external, chitinous covering, three pairs of legs, and in most groups two pairs of wings.

insecticide any substance or agent that kills insects. —**insecticidal** *adj.*

(insect) moulting hormone *(or US)* **(insect) molting hormone** *a common name for* **ecdysterone**.

insectorubin any member of a group of red or red-brown eye pigments of insects derived from oxidation products of tryptophan. *See also* **ommin**.

insectoverdin any member of a group of green pigments of insects formed of mixtures of carotenoids and biliverdin.

insert *(in genetics)* a fragment of DNA that has been linked into a cloning vector. The term can also be used as a modifier as, e.g., in **insert DNA**.

insertional inactivation the inactivation of a gene in a plasmid cloning vector by insertion of foreign DNA at endonuclease-sensitive sites. It is useful for distinguishing DNA chimeras from cleaved plasmid molecules that have self-annealed.

insertional mutagenesis the induction of a mutation by the insertion of DNA into a gene using recombinant DNA techniques. One approach, known as restriction enzyme-mediated integration (REMI), utilizes a plasmid that is cut with a restriction enzyme. Then the cut plasmid, together with the restriction enzyme, is introduced into cells (e.g. *Dictyostelium*) by electroporation. The restriction enzyme cuts the genomic DNA at sites into which the plasmid can integrate through its **sticky ends**. If the plasmid contains a suitable marker, transformants can be isolated. The gene affected can be identified because it is effectively tagged with the plasmid. If the plasmid also contains an additional marker conferring drug resistance, the gene from the transformant can be readily cloned.

insertion mutation any mutation caused by insertion of an extranumerary nucleotide residue between two successive nucleotide residues in a DNA molecule.

insertion sequence *abbr.*: IS; *see* **transposon**.

insertion vector *(in recombinant DNA technology)* any **vector** (def. 3) that has been cut with a restriction enzyme having a single target site in the centre of the vector, so that two 'arms' are generated between which foreign DNA may be inserted.

insertosome an 800–1400 bp stretch of DNA that can insert itself randomly into the chromosome of *Escherichia coli*, thereby causing polar mutations analogous to those caused by phage Mu-1.

inside-out vesicle any vesicle formed from disrupted cell or other membranes that has sealed up so that the face of the membrane that was originally on the outside is now on the inside.

in situ *Latin* in the normal, natural, original, or appropriate position.

***in situ* hybridization** a technique of **hybridization analysis** in which chromosomes *in situ* are used as the target for hybridization with radioactive or fluorescent putative complementary DNA or RNA.

insolubilize *or* **insolubilise** to render **insoluble** (def. 1), especially by coupling covalently to an insoluble matrix. —**insolubilization** *or* **insolubilisation** *n.*

insoluble **1** incapable of being dissolved (in water unless otherwise specified); of extremely low solubility. **2** incapable of being solved; having no solution.

Ins (3,4)P_2 *symbol for* 1D-*myo*-inositol 3,4-bisphosphate.

Ins (1,3,4)P_3 *symbol for* 1D-*myo*-inositol 1,3,4-trisphosphate.

Ins (1,4,5)P_3 *symbol for* 1D-*myo*-inositol 1,4,5-trisphosphate.

Ins (1,3,4,5)P_4 *symbol for* 1D-*myo*-inositol 1,3,4,5-tetrakisphosphate.

instructive theory of immunity a theory ascribing to an antigen the function in immunity of instructing or directing uncommitted cells to form new antibodies that reflect the nature of the antigen itself. *Compare* **selective theory of immunity**.

insulate to prevent, or reduce, the passage of electricity, heat, or sound to or from (something) by interposition of a (relevant) nonconducting material.

insulin *or (formerly)* **insuline** the hypoglycemic, antidiabetic, and anabolic polypeptide hormone of the endocrine portion of the mammalian pancreas or of homologous organs of lower vertebrates. In mammals, it is elaborated in the B cells of the islets of Langerhans and stored within them in the B granules prior to release by exocytosis. Insulin is a slightly acidic protein that readily aggregates to form dimers, hexamers, and higher multimers. It is very poorly soluble in aqueous media around its isoelectric point (pH ≈ 5.4), especially in the presence of certain divalent metal ions, typically Zn^{2+}, with which it can form crystals, usually containing two or four metal ions per insulin hexamer, depending on conditions. It does, however, dissolve without denaturation in organic solvents in an acid medium, a property that can be exploited in its isolation. The monomer of insulin is one of the smallest known proteins, with M_r values such as 5733 (bovine), 5777 (porcine), or 5807 (human). Bovine insulin was the first protein to have its primary sequence determined, by **Sanger** in 1955. The sequences of a large number of insulins are now known, all of which consist of two polypeptide chains, commonly termed the **A chain** and the **B chain**, with three disulfide bridges formed between half-cystine residues; two of these bridges are interchain, forming A7–B7 and A19–B20 links, and the third is intrachain, linking positions A6 and A11 to form a heterodetic ring in the A chain. The numbers of amino-acid residues vary slightly with the species of origin, commonly being 21 and 30 in the A and B chains, respectively; six amide groups are present per molecule of the monomer if insulin is carefully isolated. The three-dimensional structure is known: chains A and B have two motifs each. Insulin is structurally related to **relaxin** and **insulin-like growth factor**. Insulin is biosynthesized by post-translational modification of preproinsulin via its single-chain precursor **preproinsulin**. In preproinsulin, residues 1–24 are the signal sequence. When this is removed, proinsulin is formed. In the Golgi apparatus, prohormone convertases PC2 and PC3 cleave proinsulin on the carboxyl side of a pair of basic amino-acid residues (Arg^{55}-Arg^{56} and Lys^{88}-Arg^{89}). This excises the C peptide; (residues 57–87, leaving the A and B chains (two Arg residues (55 and 56) must first be cleaved from the B chain by carboxypeptidase H for the mature B chain to be formed). Residues 55–87 are known as the connecting peptide. Example (human): database code INS_HUMAN, 110 amino acids (11.97 kDa); the A chain is derived from residues 90–110, and the B chain from residues 25–54.

Insulin stimulates glucose uptake by muscle and adipose tissue, and promotes glycogenesis, lipogenesis, and synthesis of protein and nucleic acid. Deficiencies in the secretion or action of insulin in humans result in the overproduction and increased urinary excretion of glucose (*see* **glucose-tolerance test**, **diabetes mellitus**); continuing therapeutic administration of insulin is necessary in type I (insulin-dependent) diabetes

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mellitus. Commercial insulin for therapeutic use is extracted mostly from bovine or porcine pancreas; human insulin is now also being made by recombinant DNA technology. The international unit for insulin is defined as the activity contained in 0.041 67 mg of the Fourth International Standard for Insulin, Bovine and Porcine, for Bioassay (which is defined as crystalline zinc insulin derived from a mixture of 52% bovine insulin and 48% porcine insulin).

insulinase EC 3.4.99.45; *other names*: insulin-degrading enzyme; insulin protease; an enzyme that catalyses the degradation of insulin and glucagon, progressively cleaving a number of peptide bonds in insulin, but only Arg^{17}-|-Arg^{18} in glucagon.

insulin-dependent diabetes mellitus *abbr.*: IDDM; *see* **diabetes mellitus**.

insulin-like activity *abbr.*: ILA; *a provisional name given to* material thought to be present in plasma or serum that showed apparently higher insulin levels when measured by the rat epididymal fat-pad assay than when other *in vitro* assay methods were used; it was found to be due to **insulin-like growth factor**.

insulin-like growth factor *abbr.*: IGF; any member of a group of polypeptides that are structurally homologous to ***insulin*** and share many of its biological activities but are immunologically distinct from it; they are mitogens of the insulin/relaxin family. They include substances now named insulin-like growth factor-I (IGF-I), which is a monomer of 70 amino acids, and insulin-like growth factor-II (IGF-II), which is a monomer of 67 amino acids; together these were formerly known as **nonsuppressible insulin-like activity** (NSILA). The insulin-like growth factors also include **somatomedin** C, which is IGF-I, and possibly also somatomedins A_1 and A_2, and **multiplication-stimulating activity**. They appear to be more potent than insulin as growth-promoting factors but less potent in stimulating glucose utilization. Brain IGF is a truncated form of IGF-I, in which the N-terminal tripeptide sequence is lacking. Example, (precursor) human IGF-II: database code IGF2_HUMAN, 180 amino acids (20.12 kDa). *See also* **insulin-related growth factor**, **somatomedin**.

insulin-like growth factor binding protein *abbr.*: IGFBP; any of several proteins that bind insulin-like growth factors (IGFs) and are found in serum, amniotic and other body fluids, and in conditioned media from a variety of cell types. They are believed to prolong the half-life and regulate the endocrine effects of IGFs. Six IGFBPs (IGFBP-1 to -6) have been identified in humans, their complementary DNA having been cloned and sequenced. IGFBP-1 was originally identified as a placental protein, placental protein-12 (PP-12) and as α-1 pregnancy-associated globulin; it is a nonglycosylated protein of M_r 25 000; IGFBP-2 has been identified in human and rat central nervous systems; it is a nonglycosylated protein of M_r 31 000. IGFBP-1 and IGFBP-2 both have the RGD motif, a recognition site for **integrins**. IGFBP-3 is the principal IGFBP in human serum; it is a glycoprotein of M_r 28 500, and circulates as a complex with IGF peptide (γ subunit). For IGFBP-5 *see* **skeletal growth factor**.

insulinogenesis the formation of **insulin**.

insulinogenic *resulting from the administration of* ***insulin***.

insulinoma any neoplasm (benign or malignant), originating in the B cells of the pancreatic islets (or sometimes from non-islet tissue), that autonomously secretes insulin and/or biosynthetic precursors of insulin. Such lesions are frequently recognized by their metabolic consequences.

insulinotropic stimulating **insulin** secretion.

insulinotropic effect *see* **gastric inhibitory peptide**.

insulinotropin a peptide containing residues 7–37 of glucagon-like peptide I, coencoded with glucagon in preproglucagon. It is a potent stimulator of insulin release from the perfused rat pancreas. *See* **glucagon-like insulinotropic peptide**.

insulin receptor a type I membrane protein with tyrosine kinase (EC 2.7.1.112) activity. The protein is derived from a precursor; after being transported from the endoplasmic reticulum to the Golgi apparatus, the single glycosylated precursor is further glycosylated and then cleaved to α and β chains. In the plasma membrane the receptor is a disulfide-bonded heterotetramer, $\alpha_2\beta_2$; the α chains are entirely extracellular, while each β chain has one transmembrane domain. The ligand binds to the α-subunit extracellular domain and the kinase is associated with the β-subunit intracellular domain; it is partly regulated by autophosphorylation. Associated diseases include various forms of insulin resistance, including type 2 **diabetes mellitus** and **leprechaunism**. Example (human precursor): database code INSR_HUMAN, 1382 amino acids (156.10 kDa); amino acids 28–762 form the α subunit, 763–1382 form the β subunit.

insulin-related growth factor *(sometimes)* any of a group of vertebrate and invertebrate protein or polypeptide hormones or growth factors (including **relaxin**, **nerve growth factor**, **insulin-like growth factors**, silkworm prothoracicotropic hormone, and possibly others) that share with insulin certain features of primary and three-dimensional structure and may also display some similarities to insulin as regulators of growth and/or metabolism.

insulin-tolerance test a sensitive and accurate test of the integrity of the hypothalamic–pituitary–adrenal axis and its ability to respond to stress, and also of somatotropin responsiveness. The test is performed after an overnight fast with measurement of plasma cortisol, glucose, and somatotropin levels before and periodically after intravenous administration of insulin. The hypoglycemia induced by insulin elicits a potent stress response via the central nervous system, stimulating the release of **corticotropin releasing hormone** and consequently, of **corticotropin**.

Int the product of phage gene *int*, involved in the integration of phage DNA into host DNA during transition from the lytic to the lysogenic states of the phage. *Compare* ***Int-2***. *See also* **retroregulation**.

Int-2 an oncogene first identified as a transforming gene following the integration of mouse mammary tumour virus into the mouse DNA. Its product has been shown to be a **fibroblast growth factor** (FGF3). Example (precursor): database code FGF3_HUMAN 239 amino acids (26.89 kDa). *Compare* **Int**.

integer any rational whole number.

integral **1** of, or being an essential part of a whole; entire, complete. **2** *(in mathematics)* of, or denoted by, an **integer**; of or involving an **integral** (def. 3). **3** *(in mathematics)* the sum of a large number of infinitesimally small quantities, denoted ∫, summed either between specified limits (**definite integral**) or within indeterminate limits (***indefinite integral***).

integral (cell membrane) protein *or* **intrinsic protein** *an operational term for* any protein that can only be dissociated from a cell membrane by drastic treatment with a reagent such as detergent, bile salt, protein denaturant, or organic solvent. Such proteins have one or more domains that traverse the cell membrane. *Compare* **peripheral (cell membrane) protein**.

integrase a protein of lambdoid phages that catalyses integration of phage DNA during establishment, probably by forming a transient DNA–protein link. Example from phage lambda: database code VINT_LAMBD, 356 amino acids (40.26 kDa). The same enzyme is one subunit of the **excisase** activity that reverses this; the other subunit is the Xis protein, known as **excisionase**. Example from phage lambda: database code VXIS_LAMBD, 72 amino acids (8.60 kDa).

integrate **1** to combine or be combined into a whole; to complete (something imperfect) by the addition of parts. **2** *(in mathematics)* to find the **integral** (def. 3) of (quantities, expression, etc.). **—integrable, integrative** *adj.*; **integrability** *n.*

integrated rate equation a general expression for the interpretation of a single enzyme-catalysed reaction. The expression for the velocity of a reaction at time t is:

$$v = d[P]/dt = V([S]_0 - [P]_t)/\{K_m + ([S]_0 - [P]_t)\}.$$

This can be integrated with respect to time to give:

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$$Vt = [P]_t + K_m \ln\{[S]_0/([S]_0 - [P]_t)\},$$

or

$$\ln\{[S]_0/([S]_0 - [P]_t)\}/t = V/K_m - [P]_t/K_m t,$$

where [S] and [P] are the concentrations of substrate and product, v is the velocity of the reaction, V is the limiting rate, and K_m is the Michaelis constant. The subscripts indicate the concentrations at zero time and at time t. A plot of $\ln\{[S]_0/([S]_0 - [P]_t)\}/t$ against $[P]_t/t$ will have a slope of $-1/K_m$ and an intercept of V/K_m.

integration **1** the act or process of uniting or adding parts to make a whole. **2** the process of determining and/or indicating the mean value or total sum of (some physical quantity, area, etc.). **3** *(in mathematics)* the process of determining the **integral** (def. 3) of a function or a variable. *Compare* **differentiation**. **4** *(in genetics)* the act or process of forming a **cointegrate**.

integrator any device (mechanical or electronic) or any person that determines the value of an **integral** (def. 3).

integrin any member of the large family of transmembrane proteins that act as receptors for **cell-adhesion molecules**. Integrins are heterodimeric molecules in which the α and β subunits are noncovalently bonded. The subunits are named from α_1 to α_8, α_L (for **LFA-1**), α_M (for **Mac-1**), α_v (for **vitronectin** receptor), and from β_1 to β_7. Both subunits penetrate the cell-membrane lipid bilayer; the α subunit has four Ca^{2+}-binding domains on its extracellular chain, and the β subunit bears a number of cysteine-rich domains extracellularly. The integrins are grouped into families: the VLA family, having the β_1 subunit; the LEUCAM family, which includes LFA-1 and Mac-1, having the β_2 subunit; and a group of other integrins having subunits β_3–β_8. The type of integrin expressed on the cell surface determines which adhesion molecules (and thus which other cells) the cell will bind, and can be varied in different circumstances. For example, transforming growth factor-β increases expression of $\alpha_1\beta_1$, $\alpha_2\beta_1$, $\alpha_3\beta_1$, and $\alpha_5\beta_1$ integrins on fibroblasts and the $\alpha_v\beta_3$ integrin on fibroblasts and osteosarcoma cells; interleukin-1β enhances β_1 expression on osteosarcoma cells; and in response to wounding, the keratinocyte, which normally expresses integrin $\alpha_6\beta_4$, will express $\alpha_5\beta_1$ (VLA-1, the fibronectin receptor) so that the keratinocyte will then migrate over fibronectin in the cell matrix, thus covering the wound. Example, integrin α1 precursor from *Rattus norvegicus*: database code ITA1_RAT, 1180 amino acids (130.81 kDa); residues 1–28 are the signal peptide, 29–1180 integrin α_1. *See also* **adhesion molecules** (for details of the integrins to which they bind).

intein *a proposed term for* an internal peptide sequence of a protein precursor that is spliced out by transpeptidation during processing to form the mature protein. The peptide sequences that are spliced together are termed **exteins**. The terms are derived, respectively, by analogy from **introns**, the nucleotide sequences that are removed during mRNA processing in eukaryotes, and **exons**, the coding sequences that are spliced together to form the mature mRNA transcript.

intensify *(in photography)* to increase the opacity (of a film or plate). —**intensification**, **intensifier** *n.*

intensity *(in physics)* the magnitude of an energy flux, field strength, or force. *See* **luminous intensity**, **radiant intensity**.

intensity millicurie *an obsolete name for* **sievert** (def. 2).

intensive property any of the properties of a substance or object that describe a specific characteristic of the substance or object in a given state. Intensive properties are independent of the amount of the substance or the size of the object being considered, e.g. density, specific volume, temperature, etc. *Compare* **extensive property**. *See also* **intensive**.

inter+ *comb. form* signifying between, within, or among. *Compare* **intra+**

interaction **1** any reciprocal or mutual action or effect. **2** *(in physics)* the transfer of energy between elementary particles, between particles and a field, or between two or more fields. —**interact** *vb.*

interaction broadening the concentration-dependent broadening of lines in an electron spin resonance spectrum caused by magnetic interactions between paramagnetic molecular or atomic species.

interactive *(of two or more forces, fields, processes, etc.)* acting reciprocally or in close and/or continuing relation with each other; interacting.

interallelic complementation interaction between products of two mutant alleles to form a functional protein. It can occur in the case of multimeric proteins, for which subunits are encoded by two alleles. If products from only one mutant allele compose the protein, an inactive protein results, but in certain cases, if the products from the two alleles (each of which codes for an inactive protein) are combined in the protein, an active protein results. This was first shown in *in vitro* experiments by taking two inactive proteins of alleles encoding glutamate dehydrogenase ($NADP^+$), and recombining them by freezing and thawing in the presence of NaCl to form an active enzyme. There is some evidence that it can also occur *in vivo*.

interband any DNA-poor region between two (DNA-rich) bands in a polytene chromosome.

intercalary deletion *see* **deletion**.

intercalary DNA *abbr.*: iDNA; moderately repetitive DNA sequences occurring between structural genes in chromosomal DNA.

intercalation *(in molecular biology)* the insertion of additional material between the parts of an existing series, especially the insertion of molecules of antibiotic substances (e.g. actinomycin D) or acridine dyes (e.g. proflavine) between adjacent base pairs in a DNA duplex, thereby interfering with replication, etc. —**intercalate** *vb*; **intercalation** *n.*; **intercalary** *or* **intercalative** *adj.*

intercalator *or* **intercalating agent** *(in molecular biology)* any substance capable of being intercalated.

intercellular between cells. *Compare* **intracellular**.

intercept *(in mathematics)* a point at which two figures intersect; the point at which a line, curve, or surface cuts a coordinate axis.

interchain *(of any interaction or linkage)* between two chains of a biopolymer.

interconvertible enzyme any enzyme that exists in at least two well-defined reversibly convertible forms, produced by covalent modifications of amino-acid side chains under biological conditions (covalent modifications occurring as intermediates in the catalytic process are excluded). *Compare* **isoenzyme**.

intercrine *an alternative name for* **chemokine**.

interdomain *(of any interaction or linkage)* between two domains of a protein or other biopolymer.

interface **1** any surface forming a common boundary between two bodies, molecules, liquids, or phases. **2** any device, instrument, or method connecting two systems or processes; used especially of connections between computer systems. **3** to connect with or by an **interface** (def. 2). —**interfacial** *adj.*

interfacial tension the surface tension occurring at the interface between two mutually saturated liquids that tends to contract the area of the interface.

interference **1** *(in physics)* the process in which two or more wave trains of the same frequency and phase are superimposed to form a wave train in which there are alternate bands (called **interference fringes**) of no energy (due to **destructive interference**) or higher energy than that of the individual wave trains (due to **constructive interference**). **2** *(in virology)* the partial or complete prevention of the replication of one virus in a cell or tissue by the concomitant interaction between the given cell or tissue and another virus.

interference (light) filter a type of (light) filter with which a transmitted band-width of 10–20 nm can be obtained with a peak transmission of about 40%. It is possible to make inter-

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ference filters in which the position of the centre of the transmittted band can be set within 1–2 nm.

interference fringe *see* **interference** (def. 1).

interference optics a system of optics, based on the Rayleigh interferometer, that is sometimes fitted to analytical ultracentrifuges. A double-sector ultracentrifuge cell is used, one sector containing only solvent and the other the solution being examined. The pattern of interference fringes produced by light passing through both sectors is a function of the refractive index at each point in the cell, each fringe tracing a curve of the refractive index against distance. Interference optics allows smaller changes in concentration to be detected than is possible by the **Schlieren method**.

interferogram a photographic record of a pattern of interference fringes.

interferometer an instrument that divides a beam of electromagnetic radiation into a number of beams and reunites them to produce **interference** fringes. It is useful for accurate measurement of the wavelength of the radiation, examination of the hyperfine structure of spectral lines, the testing of the flatness of surfaces, etc. —**interferometric** *adj.*; **interferometrically** *adv.*; **interferometry** *n.*

interferon *abbr.*: IFN; any member of a group of proteins that form a closely related group of nonviral proteins, of M_r in the range 15 000 to 30 000, that are produced and liberated by animal cells following exposure to a variety of inducing agents; they are not normally present in uninduced cells. They exert nonspecific, antiviral activity, at least in homologous cells, through cellular metabolic processes involving the synthesis of both RNA and protein. Viruses are the most potent inducing agents, but interferons can also be induced by exposure of cells to a wide variety of microorganisms, bacterial endotoxins, phytohemagglutinins, and other substances. Interferons do not prevent viral penetration into cells but induce within the cells a complex of inhibitors of protein synthesis that block translation of viral mRNA, but not the cell's own mRNA. Among the interferon inhibitors are a protein kinase, which phosphorylates an initiation factor in protein synthesis, and an oligonucleotide synthetase, which catalyses the synthesis of pppA2′p5′A2′p5′A (*abbr.*: 2,5-A) – this trinucleotide activates a latent cellular endonuclease that degrades the viral mRNA. Interferons are classified into three types. **IFN-α** (*formerly* leukocyte interferon) comprises many examples; they are produced by macrophages, have antiviral activities, and stimulate production of two enzymes: a protein kinase and an oligoadenylate synthetase; they exist as monomers. Example, (human) α-4B precursor: database code INA4_HUMAN, 189 amino acids (21.78 kDa). **IFN-β** (*formerly* fibroblast interferon) has antiviral, antibacterial, and anticancer activities. It is related to the α family (three motifs). Example (human, precursor): database code INB_HUMAN, 187 amino acids (22.27 kDa). **IFN-γ** (*formerly* immune interferon) is produced by lymphocytes activated by specific antigens or mitogens. In addition to antiviral activity it has important immunoregulatory functions: it is a potent activator of macrophages, it has antiproliferative effects on transformed cells, and can potentiate the antiviral and antitumour effects of the type I interferons (α and β). It is a glycoprotein and exists as a homodimer. Example (human, precursor): database code ING_HUMAN, 166 amino acids (19.33 kDa). Interferons are produced commercially either by *in vitro* culture of human leukocytes or by recombinant DNA or RNA technology, γ interferon requiring a system that effects glycosylation.

intergenic suppression *see* **suppression**.

interjacent RNA a 26S single-stranded RNA found in cells infected with certain togaviruses, e.g. Semliki forest virus. It codes for all the virus coat proteins.

interleukin *abbr.*: IL; any member of a heterogeneous group of **cytokines** that have the ability to act as signalling molecules between different populations of leukocytes. Several classes have been defined; each is designated by a suffixed arabic numeral, e.g. **interleukin 1** (IL-1), **interleukin 2** (IL-2), etc.

interleukin 1 *abbr.*: IL-1; *former names*: lymphocyte-activating factor (LAF); mitogenic protein (MP); helper-peak-1 (HP-1); T-cell-replacing factors III and m (TRF-III; TRF-m); B-cell-activating/differentiation factor (BAF; BDF). An interleukin of M_r 12 000–18 000, produced mainly by activated macrophages. It is not able to promote and maintain *in vitro* long-term cultures of T cells, but stimulates thymocyte proliferation by inducing **interleukin 2** release. It is involved in the inflammatory response, and is identified as an endogenous pyrogen. Example, IL-1β (human): database code NRL1_6I1B, 153 amino acids (17.36 kDa); 3-D structure data obtained by NOESY.

interleukin 2 *abbr.*: IL-2; *other names*: thymocyte-stimulating factor (TSF); thymocyte mitogenic factor (TMF); T-cell growth factor (TCGF); co-stimulator; killer-cell helper factor (KHF); secondary cytotoxic T-cell-inducing factor (SCIF). An interleukin of M_r 30 000–35 000, produced by T cells in response to antigenic or mitogenic stimulation. Translocation involving the IL-2 gene causes one form of acute lymphoblastic leukemia. IL-2 promotes and maintains *in vitro* long-term cultures of T cells. Example, human (precursor): database code IL2_HUMAN, 153 amino acids (17.61 kDa).

interleukin 3 *abbr.*: IL-3; *other names*: multipotential colony-stimulating factor; hematopoietic growth factor; P-cell-stimulating factor; mast-cell growth factor. A class of interleukins that are granulocyte/macrophage colony-stimulating cytokines; they act in hematopoiesis by controlling the production, differentiation, and function of granulocytes and the monocytes/macrophages. They are glycoprotein monomers. Example, human (precursor): database code IL3_HUMAN, 152 amino acids (17.21 kDa).

interleukin 4 *abbr.*: IL-4; *other names*: B-cell stimulatory factor 1; lymphocyte stimulatory factor 1. An interleukin that participates in at least several B-cell activation processes as well as those of other cell types. It is a co-stimulator of DNA synthesis and is a glycoprotein. Example: database code NRL_1RBC, 129 amino acids (14.95 kDa); 3-D structure known.

interleukin 5 *abbr.*: IL-5; *other names*: T-cell-replacing factor; eosinophil differentiation factor. An interleukin that induces terminal differentiation of late-developing B cells to immunoglobulin-secreting cells. It is a homodimer, with subunits linked by a disulfide bond. Example, human (precursor): database code IL5_HUMAN, 134 amino acids (15.22 kDa).

interleukin 6 *abbr.*: IL-6; *other names*: B-cell stimulatory factor 2; interferon β-2; hybridoma growth factor. An interleukin that induces myeloma and plasmacytoma growth, and nerve-cell differentiation. In hepatocytes it induces acute-phase reactants. It is a glycoprotein. Example, human (precursor): database code IL6_HUMAN, 212 amino acids (23.69 kDa).

interleukin 7 *abbr.*: IL-7; *other name*: hematopoietic growth factor. An interleukin that stimulates proliferation of lymphoid progenitor cells. It is produced by monocytes, T cells, and NK cells. Example, human (precursor): database code IL7_HUMAN, 177 amino acids (20.16 kDa).

interleukin 8 *abbr.*: IL-8; *other names*: monocyte-derived neutrophil chemotactic factor (MDNCF); T-cell chemotactic factor; neutrophil-activating protein 1 (NAP-1); lymphocyte-derived neutrophil-activating factor; protein 3-10C. An interleukin that acts as a chemotactic factor, attracting neutrophils, basophils, and T cells, but not monocytes. It is released from several cell types in response to an inflammatory stimulus. Example, human (precursor): database code NRL_3I1I, 68 amino acids (7.96 kDa); 3-D structure obtained from a combination of crystallography and NMR.

interleukin 9 *abbr.*: IL-9; *other names*: T-cell growth factor; p40 precursor. An interleukin that supports IL-2/IL-4-independent growth of helper T cells. Example, human (precursor): database code IL9_HUMAN, 144 amino acids (15.89 kDa).

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interleukin 10 *abbr.*: IL-10; *other names*: cytokine synthesis inhibitory factor (CSIF); cytokine glycoprotein. An interleukin that appears to be a suppressor factor for Th1 immune responses. Example, human (precursor): database code IL10_HUMAN, 178 amino acids (20.48 kDa).

interleukin 11 *abbr.*: IL-11; *other name*: adipogenesis inhibitory factor (AGIF). An interleukin that acts as both cytokine and growth factor. It stimulates plasmacytoma proliferation, and the T-cell-dependent development of immunoglobulin-producing B cells. Example, human (precursor): database code IL11_HUMAN, 199 amino acids (21.40 kDa).

interleukin 12 *abbr.*: IL-12; *other name*: cytotoxic lymphocyte maturation factor. An interleukin that can act as a growth factor for activated T and natural killer (NK) cells, enhance the lytic activity of NK/lymphokine-activated killer cells, and stimulate the production of interferon-γ by resting PMBC. It is a disulfide-linked heterodimer of 40 kDa and 35 kDa subunits. NK stimulatory factor (NKSF) is essentially a complex of cytokine and soluble receptor. Examples, human; precursor for the 35 kDa (α) subunit: database code I12A_HUMAN, 219 amino acids (1–22 signal) (24.82 kDa); precursor for the 40 kDa β subunit: database code I12B_HUMAN, 328 amino acids (1–22 signal) (37.13 kDa). Both subunits are glycoproteins; α has some similarity to **interleukin 6**; β has an immunoglobulin-like domain.

interleukin 13 *abbr.*: IL-13; an interleukin that inhibits inflammatory cytokine production. It synergizes with **interleukin 2** in regulating interferon-γ synthesis. Example, human (precursor): database code IL13_HUMAN, 199 amino acids (21.40 kDa).

interleukin 1β convertase EC 3.4.22.36; *other name*: interleukin -1β converting enzyme (*abbr.*: ICE); a proteolytic enzyme that cleaves the interleukin-1β precursor specifically at Asp^{116}-|-Ala^{117} and Asp^{27}-|-Gly^{28} in the precursor, producing the mature cytokine. It is a cysteine endopeptidase. Example from human: database code I1BC_HUMAN, 404 amino acids (45.16 kDa).

intermediary metabolism the chemical pathways by which molecules and structures found in living cells are synthesized from molecules that are taken into the cells, and subsequently broken down to molecules that are eliminated from the cells.

intermediate **1** occurring, or situated between two things in time, place, or order. **2** *(in chemistry or biochemistry)* any compound that takes part in a reaction, or sequence of reactions, occurring between the starting materials and the products. In metabolism, intermediates occur between the nutrients taken in and cellular material synthesized, or between cellular material and excretory products.

intermediate body *a former name for* **amboceptor**.

intermediate-density lipoprotein *abbr.*: IDL; one of the classes of lipoproteins found in blood plasma in many animals (data normally relate to humans). These lipoprotein particles have diameter 19.6–22.7 nm, solvent density for isolation (g mL^{-1}) 1.006–1.019, hydrated density (g mL^{-1}) 1.003. Their approximate composition (% by weight) is 8% unesterified cholesterol, 22% esterified cholesterol, 25% phospholipid, 30% triacylglycerol, 15% protein. Their apolipoprotein composition (% by weight total apolipoprotein) is 50–70% B-100, 5–10% C-I + C-II + C-III, 10–20% E-II + E-III + E-IV. They are formed in the plasma from very-low-density lipoproteins as a result of the action of **lipoprotein lipase**, and represent an intermediate stage in the conversion of very-low-density lipoproteins to low-density lipoproteins. *See also* **apolipoprotein** for individual apolipoproteins.

intermediate filament a distinct elongated structure, characteristically 10 nm in diameter, that occurs in the cytoplasm of higher eukaryotic cells. Intermediate filaments form a fibrous system, composed of chemically heterogeneous subunits and involved in mechanically integrating the various components of the cytoplasmic space. Intermediate filaments may be divided into five chemically distinct classes: **keratin** filaments of mammalian epithelial cells; **desmin** filaments found in cells of muscles of all types; **vimentin** filaments found in mesenchymal cells; neurofilaments of neurons; and glial filaments found in all types of glial cells. *Compare* **microfilament, microtuble**.

intermediate lobe *or* **intermediate part** *or* **pars intermedia (hypophyseos)** the part of the **pituitary gland** lying between the anterior and the posterior lobes. It is absent in adult humans but is present in fetal humans and in certain other species.

intermedin *a former name for* β-melanocyte-stimulating hormone (so-called because of its occurrence in the intermediate lobe of the pituitary gland). *See* **melanocyte-stimulating hormone**.

internal compensation the phenomenon of the existence of **internally compensated** molecular entities in general, or the property of such a molecular entity in a particular instance.

internal conversion *abbr.*: IC; a mode of radioactive decay of an excited atomic nucleus (formed by a nuclear transformation) in which, in a proportion of instances, excess energy released from the nucleus is not radiated from the atom as a quantum of low-energy gamma radiation but is imparted to one of the inner orbital electrons, which is thereupon ejected as a **conversion electron**; the electron emission is homoenergetic. The filling of the vacant orbital in the resultant excited ion causes emission also of either an Auger electron or a quantum of the characteristic X-radiation of the daughter atom.

internal energy *symbol*: U *or* E; a function of state that describes the sum of the kinetic and potential energy of a system. For closed systems, a change in internal energy, ΔU, usually results in a transfer of work or heat between the system and the surroundings. Thus $\Delta U = q + w$, where q is the heat gained by the system and w is the work done on the system.

internal indicator any indicator substance used to follow a reaction, or other process, that is placed in the reaction mixture, or system.

internalize *or* **internalise** to render internal; especially to take a substance into a cell or organism. —**internalization** *or* **internalisation** *n.*

internally compensated describing any molecular entity that possesses equal numbers of structurally identical groups of opposite chirality. If no other chiral groups are present the overall entity is achiral and is designated by the prefix *meso+*.

internal secretion *a former name for* **endocrine** (def. 2).

internal standard any standard used as a reference in an assay that is added to the samples and subjected to the whole of the procedures applied to them.

internal-standard method (of quench correction) *or* **internal standardization** a method of correcting for quenching in **liquid scintillation counting**. After the sample has been counted a measured small amount of a (nonquenching) standard preparation, of known activity, of the radionuclide in question is added to it and the sample is recounted. From the increment in the count rate the counting efficiency within the sample, and hence the degree of quenching, may be calculated. The method is simple and reliable and corrects adequately for all types of quenching but is more time-consuming than the **external-standard method** and has other disadvantages.

International Biological Standard any of the numerous internationally agreed standards of activity or potency of antisera, hormones, vitamins, antibiotics, and other biologicals. Each has been defined in terms of a mass of an appropriate standard preparation, prepared and stored under specified conditions.

International Practical Temperature Scale *abbr.*: IPTS; *see* **temperature**.

International System of Units the English translation of Système International d'Unités; *see* **SI**.

International Unit *abbr.*: IU (preferred) *or* i.u. *or* u; any unit of activity or potency of an antiserum, hormone, vitamin, antibiotic, or other biological defined in terms of the activity of an appropriate **International Biological Standard** or International Biological Reference Preparation. International Units are useful for quantifying a specific biological activity of a

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material before the chemical nature of the substance responsible for the activity has been fully characterized, or before pure preparations with reproducible activity are available.

Internet a protocol for allowing communication between computers, including those at distant sites. More loosely 'the internet' is used to refer to the worldwide network of such computers, including the providers of database services, discussion forums, and other communication media. *See also* **Appendix D**.

internuclear double resonance spectrometry *abbr.*: INDOR; a technique used in **nuclear magnetic resonance spectrometry** as an aid to assignment of resonances. It involves monitoring a single frequency, f_1 (usually one corresponding to a single transition), while sweeping a perturbing (decoupling) frequency, f_2, through a selected range of frequencies. Signals, negative or positive, will only appear in the INDOR spectrum when f_2 passes through a transition that has an energy level in common with the transition at f_2, making it possible to determine otherwise inaccessible chemical shifts and coupling constants.

interphase the state of a eukaryotic cell when not undergoing mitosis or meiosis. It covers the G_1, S, and G_2 phases of the **cell-division cycle**.

interpolate *(in mathematics)* to estimate a value of a function between data values already obtained or known either graphically or by calculation. *Compare* **extrapolate**. —**interpolation** *n.*

intersegment transfer a proposed mechanism for the transfer of a repressor of gene expression in a nonspecifically bound state to its target site. It involves the rapid and direct transfer of repressor from one segment of a DNA molecule to another as a consequence of the relative diffusion of these segments within the domain of the molecule.

interstice any minute space or crevice that intervenes between structures, e.g. between cells, organs, or tissues, or between atoms in a crystal lattice. —**interstitial** *adj.*

interstitial cell a connective tissue cell lying in the interstices between other cells in a tissue and serving to bind the tissue cells. Examples include the neuroglial cells and the testosterone-producing Leydig cells lying between the seminiferous tubules in the testis of vertebrates.

interstitial cell-stimulating hormone *abbr.*: ICSH; *a former name for* **luteinizing hormone**.

interstitial collagenase EC 3.4.24.7; *other names*: vertebrate collagenase; matrix metalloproteinase 1; an enzyme that cleaves preferentially one bond in native collagen and catalyses the cleavage of the triple helix of collagen at about three-quarters of the length of the molecule from the N terminus, at Gly^{775}-|-Ile^{776} in the α-1(I) chain. It cleaves synthetic substrates and α-macroglobulins at bonds where P1′ is a hydrophobic residue. Zinc is a cofactor. Example (precursor) from human fibroblasts: database code COG1_HUMAN, 469 amino acids (53.95 kDa).

interstitial deletion the loss of DNA or part of a chromosome that occupies an interstitial (i.e. nonterminal) position.

interstitial fluid the portion of the **extracellular fluid**, consisting mainly of water, that occurs outside the blood vessels and the lymphatics. In a 70 kg man its volume is approximately 12 L and it represents approximately 17% of body mass. It has a higher content of sodium, chloride, and bicarbonate and a lower content of potassium, magnesium, sulfate, and phosphate than **intracellular fluid**.

intertrabecular space the space within cells lying between the elements of the **microtrabecular lattice**.

intervening sequence *an alternative name for* **intron**.

intimin an actin-polymerization-inducing protein produced by enteropathogenic and enterohemorrhagic strains of enteric bacteria. It is an outer membrane protein of *Escherichia coli*, necessary for attachment of the bacterium to epithelial cells. Example from *Hafnia alvei*: database code HAFEAEA, 280 amino acids (30.11 kDa).

intoxication **1** any metabolic process that converts a nontoxic **xenobiotic** to a toxic product. **2** poisoning, especially with ethanol, manifested in behavioural change of the subject.

intra+ *prefix* signifying within, on the inside, or during. *See also* **endo+**. *Compare* **inter+**.

intracellular within a cell or cells.

intracellular fluid *abbr.*: ICF; the portion of the total fluid content of a multicellular organism that occurs within the cells, especially as distinct from **extracellular fluid**. In a 70 kg man the volume of ICF is approximately 26.5 L, and it represents approximately 38% of body mass. It has a higher content of potassium, magnesium, sulfate, and phosphate, and a lower content of sodium, chloride, and bicarbonate than **interstitial fluid**.

intrachain *(of any interaction or linkage)* between different parts of a single chain of a biopolymer.

intradermal *abbr. (in medicine)*: ID *or* i.d.; within the layers of the skin.

intradomain *(of any interaction or linkage)* within a single domain of a protein or other biopolymer.

intragenic suppression *see* **suppression**.

intramolecular within the same molecule.

intramolecular chaperone a domain of a protein that mediates conformation (i.e. exercises a **chaperone** function) of the protein within which it resides. **Trypsinogen**, e.g., contains such a domain.

intramuscular *abbr. (in medicine)*: IM *or* i.m.; within a muscle or muscles; used especially of an injection.

intraperitoneal *abbr.*: IP *or* i.p.; within the peritoneum; used especially of an injection, infusion, or aspiration.

intrapleural within the pleura or pleurae; used especially of an injection or aspiration.

intrathecal within the intradural or subarachnoid space; used especially of an injection or aspiration.

intravenous *abbr. (in medicine)*: IV *or* i.v.; within a vein; used especially of an injection, infusion, transfusion, or aspiration.

intrinsic **1** of or pertaining to the essential nature of something; inherent. **2** *(in morphology)* peculiar to, or situated in a part. —**intrinsically** *adv.*

intrinsic association constant *or* **intrinsic binding constant** *see* **intrinsic constant**.

intrinsic activity *an alternative name for* **maximal agonist effect**.

intrinsic birefringence the optical anisotropy of an individual molecule.

intrinsic constant any association, binding, or dissociation constant that describes the association, binding, or dissociation of a ligand to (or from) a particular site on a polyvalent molecule, when all the sites of this type are identical, present in the same molecule, and noninteracting.

intrinsic dissociation constant *see* **intrinsic constant**.

intrinsic efficacy *symbol*: ε; an expression introduced by Furchgott that denotes the notional efficacy of a drug associated with a single receptor. It is given by $\varepsilon = e/[R_t]$, where e is the **efficacy** and $[R_t]$ indicates the total concentration of active receptors of a certain type.

intrinsic factor a glycoprotein, secreted by the parietal cells of the gastric mucosa, that is necessary for the adequate absorption of dietary **cobalamins**. Intrinsic factor binds cobalamins in the intestinal lumen to form a complex that is subsequently bound by a specific receptor on the mucosa of the ileum. Cobalamin is then dissociated from the complex by a releasing factor and actively transported across the mucosa into the bloodstream. Congenital pernicious anemia seems to be due to a defect of intrinsic factor. Example (precursor) from human: database code IF_HUMAN, 417 amino acids (45.37 kDa).

intrinsic pathway (of blood coagulation) *see* **blood coagulation**.

intrinsic protein *less common term for* **integral (cell membrane) protein**.

intrinsic viscosity *symbol*: η_{int}; the limiting value of the **spe-**

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cific viscosity, η_{sp}, of a solution as the concentration of the solute tends to zero. The units are $cm^3\ g^{-1}$. Its value depends on the specific volume of the (solvated) solute, V, and on a shape-dependent factor, ν, as follows: $\eta_{int} = \nu V$. The value of ν is 2.5 for a sphere and its value increases for solutes of other shapes. The name **limiting viscosity number** has been recommended for this attribute.

intron *or* **intervening sequence** any intragenic region of DNA in eukaryotes that will not ultimately be expressed in a mature RNA molecule. Such sequences of deoxyribonucleotide residues intervene between coding sequences (**exons**); this arrangement of introns alternating with exons constitutes a **transcription unit**. By customary usage, the term is extended to the corresponding regions of the **primary transcript** of RNA. In RNA, four general types of introns are distinguishable: (1) yeast nuclear tRNA; (2) group I introns; (3) group II introns; and (4) nuclear mRNA precursor. Group I and II introns were originally described for fungal mitochondrial genes; group I introns are characterized by a lack of conserved sequences at splicing junctions but have short conserved sequences internally, while group II introns have conserved sequences at the splicing junctions. The introns of different RNA types are spliced by different mechanisms (*see* **splicing**). With respect to the function of introns it has been customary to describe them as derived from 'junk DNA' , i.e. DNA for which no function can be found, but this concept must be modified. In the case of 'self-splicing introns' in the pre-rRNA of *Tetrahymena* many of the self-splicing introns double as mRNAs from which proteins are expressed that assist self-splicing and/or mediate intron translocation to new DNA sites. In the expression of a gene coding for small, stable RNAs that accumulate in the nucleolus, certainly of humans and mouse, it is the introns that give rise to RNA rather than the exons. Hence the terms intron and exon should simply signify RNA sequences that become physically separated during the process of RNA splicing. —**intronic** *adj.*

inulin a slightly soluble polysaccharide, of ≈6 kDa, found in members of the Compositae and Campanulaceae, in which it partially or completely replaces starch as a reserve carbohydrate. It is a linear glycan composed of about 35 ($\beta2\rightarrow1$)-linked D-fructofuranose residues terminating in an ($\alpha1\rightarrow2$)-D-glucopyranosyl residue. Inulin is useful in the measurement of renal clearance, as inulin is neither reabsorbed nor secreted by the renal tubular cells. It is also useful in the measurement of extracellular fluid volume (**inulin space**), since it can pass through the blood capillary walls but is not taken up by cells.

inulobiose the disaccharide 2-*O*-β-D-fructofuranosyl-D-fructose.

inulosucrase EC 2.4.1.9; an enzyme concerned in inulin biosynthesis. *See also* **sucrase** (def. 3).

in utero *Latin* within the uterus.

in vacuo *Latin* in a vacuum.

invaginate **1** to infold, especially to form a sheathlike or saclike enclosure. **2** describing an organ or part that is folded back upon itself. —**invagination** *n.*

invariant residue any amino-acid residue that always occurs in equivalent positions in the polypeptide chains of homologous proteins from different species, or in genetic variants of the protein from a given species.

invasin *an alternative name for* **hyaluronidase**.

invasive *(in pathology)* tending to penetrate into healthy tissue and grow within the host away from the site of entry or origin. It is used especially of a pathogenic organism, cell, or group of cells, e.g. cancer cells. —**invasiveness** *n.*

inverse agonist any ligand that by binding to receptors reduces the fraction of them in an active conformation, thereby having biological effects opposite to those produced by an **agonist** (as in **benzodiazepine inverse agonist**). This can occur if some of the receptors are in the active form even in the absence of a conventional agonist. *Compare* **partial inverse agonist**.

inverse-square law a law according to which the magnitude of a physical quantity, e.g. the intensity of electromagnetic or other radiation, is proportional to the reciprocal of the square of the distance from the source of the property.

inversion **1 configurational inversion** the process of changing the **configuration** about a chiral centre into that with the opposite configuration. *See also* **Walden inversion**. **2** the hydrolysis of sucrose to an equimolar mixture of glucose and fructose. It is so-called because of the accompanying reversal of direction of optical rotation by the solution. **3 chromosomal inversion** the deletion of a chromosomal segment followed by its reinsertion at the same position after having been turned through 180°.

inversion isomer *an alternative name for* **invertomer**.

invert **1** to turn or cause to turn inward, or upside down. **2** to reverse in direction, sequence, effect, etc. *See also* **inversion**.

invertase *or* **saccharase** EC 3.2.1.26; *recommended name*: β-fructofuranosidase; *systematic name*: β-D-fructofuranoside fructohydrolase. An enzyme from yeast and other sources that catalyses the **inversion** (def. 2) of sucrose. *See also* **saccharase**.

invertase *another name for* **β-fructofuranosidase**.

invertebrate **1** any animal lacking a vertebral column (backbone) and internal skeleton. **2** of, pertaining to, or designating any such animal.

inverted repeat *or* **indirect repeat** *abbr.*: IR; either of a pair of sequences in duplex DNA that exhibit two-fold rotational symmetry around a centre, the two sequences being complementary to each other. The sequence of the two repeats together is called a **palindrome**, e.g.

GGTACC
CCATGG.

The repeats need not be contiguous, e.g.

GGTNNACC
CCANNTGG.

Inverted repeats promote the formation of **cruciform** structures. Their function is unknown. However, they are found flanking transposable elements, which may indicate an associated role. *See also* **cruciform**, **dyad symmetry**, **hairpin**.

invertin a ferment (enzyme preparation) from yeast used by **Fischer** in work that led to his **lock-and-key model**. The major component is an α-glucosidase activity. *See also* **emulsin**.

invertomer *or* **inversion isomer** either of two **conformers** that interconvert by inversion at an atom possessing a nonbonding electron pair.

invert sugar an equimolar mixture of D-glucose and D-fructose formed by the hydrolysis, i.e. **inversion** (def. 2), of sucrose. It is sweeter than its parent disaccharide. *See also* **high-fructose corn syrup**.

in vitro *Latin (of any biological process, reaction, or experiment)* occurring or made to occur outside an organism, e.g. in extracts or cultures; literally it means 'in glass'. *Compare* ***in vivo***.

in vivo *Latin (of any biological process, reaction, or experiment)* occurring or made to occur within a living organism; literally it means 'in life'. *Compare* ***in vitro***.

involucrin a protein of keratinocytes and other stratified squamous epithelia that first appears in the cell cytosol, but ultimately becomes cross-linked to membrane proteins by the action of transglutaminase. Example from human: database code INVO_HUMAN, 585 amino acids (68.39 kDa).

involute **1** involved, intricate. **2** spiral, having whorls wound closely around the axis. **3** having edges that roll under or inwards. **4** to be subjected to a process involving the inward rolling of the surrounding tissue

iod+ *a variant form of* **iodo+** (sometimes before a vowel).

iodate **1** the anion, IO_3^-, derived from iodic(v) acid. **2** any salt of iodic(v) acid.

iodide **1** the anion, I^-, of the element iodine. **2** any salt of

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hydriodic acid. **3** any compound containing an iodine atom in organic linkage.

iodimetry a volumetric method of analysis applicable to substances with a redox potential appreciably lower than that of the iodine–iodide system (E^{o} = +0.535 V at 25 °C). Such substances are oxidized by iodine and may therefore be titrated in acid solution with a standard solution of iodine. *Compare* **iodometry**. —**iodimetric** *adj.*; **iodimetrically** *adv.*

iodinatable capable of being converted into an iodo derivative. The term may be used of an organic compound or a particular part of one, such as a residue in a peptide.

iodinate **1** to treat or react (a substance) with iodine. **2** to introduce one or more iodo groups into (an organic compound), whether by addition or substitution. —**iodination** *n.*

iodine **1** *symbol*: I; a nonmetallic element of group 17 of the IUPAC **periodic table** and one of the halogens; proton number 53; it exists naturally as a single stable nuclide, **iodine-127**, of relative atomic mass 126.904. It is widely distributed in nature, although never found as the free element, and is an essential dietary element. Numerous (about 29 unstable and seven metastable) artificial radioactive nuclides are known. Of these, the most widely used in biochemistry and molecular biology are **iodine-125** and **iodine-131**. **2** *symbol*: I_2; *the common name for* the substance correctly known as diiodine, a bluish-black solid that sublimes at room temperature into a violet-coloured irritating vapour. An ethanolic solution is useful as a mild topical antiseptic.

iodine-125 the artificial radioactive nuclide $^{125}_{53}I$. It decays to the stable nuclide tellurium-125 by capture to the nucleus of an orbital electron from the K (i.e. innermost) shell, emitting low-energy gamma radiation (35.5 keV, 7% emitted and 93% internally converted) and characteristic tellurium K X-radiation (27–32 keV, 140%), but no beta radiation. It has a half-life of 59.6 days.

iodine-127 the stable nuclide $^{127}_{53}I$. Its relative abundance in natural iodine is 100 atom percent.

iodine-131 the artificial radioactive nuclide $^{131}_{53}I$. It decays to the stable nuclide xenon-131, emitting a moderate-energy electron or beta particle of various energies (0.25–0.81 MeV max., mainly 0.61 MeV max.) plus gamma radiation of various energies (0.08–0.72 MeV, mainly 0.36 MeV), 1.3% of nuclides decaying via the metastable nuclide xenon-131m. It has a half-life of 8.04 days.

iodine-labelling a widely used procedure for labelling a compound or material by introducing into it, directly or indirectly, one or more atoms per molecule of iodine, especially radioactive isotopes (i.e. radioiodine). *See also* **radioiodinate**.

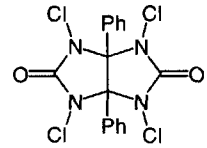
iodine number *or* **iodine value** a measure of the degree of unsaturation of a fat or fatty acid, defined as the number of grams of iodine capable of reacting with 100 g of the sample. It is usually determined indirectly by measuring the amount of an iodine-containing reagent, e.g. iodine monobromide, that remains after excess has been added and reaction is complete. The iodine number of saturated fatty acids is zero, that of oleic acid is 90, of linoleic acid 181, and of linolenic acid 274.

iodo of, relating to, or describing a compound that contains an iodine atom in organic linkage.

iodo+ *or (sometimes before a vowel)* **iod+** *comb. form* denoting **1** an iodine atom in organic linkage. **2** violet-coloured. *See also* **iodo**.

iodoacetamide $I–CH_2–CONH_2$; a compound that acts as an inhibitor of an enzyme containing –SH groups, Enz–SH, by reacting irreversibly to give $Enz–S–CH_2–CONH_2$, with elimination of HI.

Iodo-Gen *a proprietary name for* 1,3,4,6-tetrachloro-3α,6α-diphenylglycouril; a solid-phase reagent that oxidizes low concentrations of inorganic iodide to iodine and hence is useful for the rapid and efficient labelling of proteins with radioactive iodine. Being very stable and virtually insoluble in water, it can be used in the form of a prior coating on the walls of a reaction vessel containing aqueous solutions of iodide ion and protein.



iodogorgoic acid *a former name for* 3,5-**diiodotyrosine**.

iodometry a volumetric method of analysis applicable to substances with a redox potential appreciably higher than that of the iodine–iodide system ($E^{o\prime}$ = +0.535 V at 25 °C). Such substances are reduced by iodide, which is added in excess to acidified solutions and the liberated iodine titrated with a standard solution of thiosulfate. *Compare* **iodimetry**. —**iodimetric** *adj.*; **iodimetrically** *adv.*

iodopsin any of three light-sensitive visual pigments in the cone cells of the retinas of vertebrates other than freshwater and migratory fishes and some amphibians. They consist of different cone-type opsins combined (as Schiff's bases) with 11-*cis*-**retinal**. Each individual cone cell contains one of the three pigments, which have absorption maxima at ≈430 nm, ≈540 nm, and ≈575 nm. The iodopsins were once thought to be a single pigment, termed visual purple or visual violet. *See also* **cyanopsin**, **retinal**.

ion any atom or other molecular entity that has acquired an electric charge by loss or gain of one or more electrons. An anion is negatively charged, and a cation is positively charged.

ion atmosphere the region surrounding a charged molecular entity in which there is a statistical preference for ions of opposite charge.

ion chamber *another name for* **ionization chamber**.

ion channel any of several types of channels in cell membranes that allow the passage of specific inorganic ions through the membrane. They may be **ligand-gated**, or **voltage-gated**. In other cases, an ion channel may be opened by mechanical stress (**mechanically gated channels**). For ligand-gated channels, the ligand may be an extracellular mediator such as a neurotransmitter (**transmitter-gated channel**), or an intracellular mediator such as an ion (**ion-gated channel**) or a nucleotide (**nucleotide-gated channel**). Ion channels are common direct or indirect targets for the action of drugs, which may either potentiate or inhibit channel opening.

ion exchange the process in which ions of like charge, which may be the same or different chemically, are exchanged between two phases, such as two solutions separated by a semi-permeable membrane or a solution and an insoluble material, e.g. a resin.

ion-exchange cellulose *abbr.*: IEC; any derivatized cellulose containing cationic or anionic substituents used in **ion exchange**, especially for the separation of charged biopolymers.

ion-exchange chromatography any form of chromatography that depends on the process of **ion exchange** to effect the separation.

ion exchanger any **anion exchanger** or **cation exchanger**.

ion-exchange resin any insoluble polymer of high molecular mass and carrying groups with like charges that is used in **ion exchange**.

ion-exclusion chromatography a chromatographic technique by which strong electrolytes can be separated from non-electrolytes and weak electrolytes by passage of the mixture through an ion-exchange resin in a buffer of ionic strength and pH that can be varied in the course of the separation. At low salt concentrations particularly, ionic repulsive forces tend to exclude from the resin those ions that have the same charge as the functional groups on the resin so that these ions, together with an equivalent number of counterions, pass rapidly

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through the column while nonelectrolytes and weak electrolytes enter the resin and thus pass more slowly through the column at a rate determined in part by the pK of their ionizable groups.

ion-gated channel *see* **ion channel**.

ionic 1 of, pertaining to, existing as, or characterized by **ions**. 2 using or operated by ions.

ionic atmosphere the cloud of ions of one charge type that tend to accumulate by interionic attraction around an ion of the other charge type in a solution of an electrolyte. The cloud is symmetrical about the charge on the central ion unless the solution is subjected to a shearing force conducive to flow or is exposed to an applied electric field. In the latter event the central ion and its surrounding counterions migrate in opposite directions, the resultant asymmetric disposition of the ionic atmosphere effecting retardation of the central ion in a concentration-dependent manner.

ionic bond any bond formed by attraction between a positively and a negatively charged group on different parts of the same molecule or on different molecules.

ionic conduction the passage of electricity due to the movement of ions.

ionic detergent any **anionic detergent** or **cationic detergent**. *Compare* **nonionic detergent**.

ionic double layer the region surrounding a charged molecular entity together with the layer of **counterions** that surrounds it.

ionic mobility a measure of the velocity at which an ion moves through a liquid under the influence of an applied electric potential.

ionic product *see* **ion product**.

ionic strength *symbol*: I *or* I_m (molality basis) *or* I_c (concentration basis); a physical quantity equal to half the summation over all ions in a solution of the concentration of each ion multiplied by the square of its charge. Hence,

$$I_m = 0.5(\Sigma m_i z_i^2)$$

and

$$I_c = 0.5(\Sigma c_i z_i^2),$$

where m_i and c_i are the molal and molar concentrations of the ith ion, respectively, and z_i is its charge.

ionizable group *or* **ionisable group** any uncharged group in a molecular entity that is capable of dissociating by yielding an ion (usually an H^+ ion) or an electron and itself becoming oppositely charged, or of associating with an ion (usually an H^+ ion) and itself assuming the ion's charge. The extent to which an ionizable group becomes an ionizing group depends on the constitution of the molecular entity and upon the environment.

ionization *or* **ionisation** any of the processes by which one or more ions are generated. It may occur, e.g., by loss or gain of a hydron by a solute in response to changes in pH, or by the loss of an electron from a neutral chemical species by unimolecular heterolysis of such a species into two or more ions. Further, a gas may become ionized by the passage through it of fast charged particles or electromagnetic radiation.

ionization chamber *or* **ionisation chamber** *or* **ion chamber** a chamber containing a gas and two electrodes between which an electric potential difference is maintained. It is used to detect ionizing particles or electromagnetic radiation by virtue of the current that flows following ionization of the gas.

ionization constant *or* **ionisation constant** the **dissociation constant** for a reversible reaction in which the products are ionic.

ionization energy *or* **ionisation energy** *symbol*: E_I; the minimum energy (enthalpy) required to remove an electron from an isolated molecular entity (in its vibrational ground state) in the gaseous phase. It was formerly, and misleadingly, termed ionization potential.

ionization potential *or* **ionisation potential** *a former term for* **ionization energy**.

ionize *or* **ionise** to convert, or to become converted, wholly or in part, into ions; to cause **ionization** of (something). —**ionizable** *adj.*

ionizing particle *or* **ionising particle** any charged particle of sufficient energy to enable it to dislodge an orbital electron from an atom or other molecular entity. *See* **ionizing radiation**.

ionizing power *or* **ionising power** *or (sometimes)* **polarity** a qualitative term used to denote the tendency of a particular solvent to promote ionization of an uncharged solute.

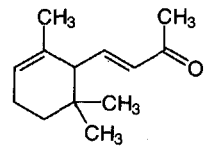
ionizing radiation *or* **ionising radiation** any radiation, corpuscular or electromagnetic, that is capable of causing **ionization** (directly or indirectly) of matter through which it passes. For ionization to occur, the kinetic or photon energy, respectively, must be greater than the **ionization energy** of the irradiated substance. Ultraviolet radiation, X-radiation, alpha particles, and high-energy electrons (including beta particles) are more effective than gamma radiation or neutrons. It is commonly known simply as radiation.

ionogen 1 any compound that can dissociate into ions in a suitable environment; an electrolyte. 2 any atom or group that is capable of becoming ionized chemically. —**ionogenic** *adj.*

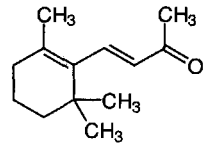
ionography *an alternative name for* **zone electrophoresis**.

ionomycin a nonfluorescent antibiotic ionophore derived from *Streptomyces conglobatus*. It is highly specific for divalent cations and exhibits greater selectivity for Ca^{2+} over Mg^{2+} than **A23187** (calcimycin). It complexes with Ca^{2+} between pH 7 and 9.5 with intense UV absorption, and thus may be used as a carrier of Ca^{2+} and for measurement of cytoplasmic Ca^{2+} concentration.

ionone either of two terpene compounds, α-ionone and β-ionone, found in a number of plants. β-Ionone is an intermediate in the synthesis of vitamin A; its odour is reminiscent of cedarwood or, in dilute alcohol solution, of violets.



α-ionone



β-ionone

ionophore *or* **ionophorous agent** any member of a varied group of both natural and synthetic substances, cyclic or linear and of greatly differing relative molecular masses, that are capable of binding metal ions in solution and transporting them across lipid barriers in natural or artificial membranes. They may be classed as **cage carriers**, when the ionophore surrounds the metal ion during transport, or as **channel carriers**, when the ionophore forms an ion-conducting pore in the membrane. —**ionophorous** *or* **ionophoric** *adj.*

ionophoresis **electrophoresis**, especially of relatively small ions. *See also* **iontophoresis**.

ionotropic describing a type of receptor that mediates its effects by regulating ion channels, in distinction from receptors that act by regulating enzymes such as adenylate cyclase or in-

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ositide-specific phospholipase C. *Compare* **metabotropic**. *See also* **excitatory amino-acid receptor**.

ion pair a pair of oppositely charged ions held together by coulombic attraction. *See also* **ionic bond**.

ion product *or (sometimes)* **ionic product** *symbol*: K_i; a measure of the tendency of an amphiprotic solvent, XH, to take up or to lose a hydron in the reaction:

$$XH + XH = XH_2^+ + X^-.$$

In such a reaction, $K_i = a_{XH_2^+} \times a_{X^-}$ where $a_{XH_2^+}$ and a_{X^-} are the activities of XH_2^+ and X^-, respectively. The ion product of water, K_W, is given by

$$K_W = a_{H_3O^+} \times a_{OH^-};\ K_W \approx 1 \times 10^{-14}\ \text{mol}^2\ \text{dm}^{-6} \text{ at } 25\ ^\circ\text{C}.$$

It has a large positive temperature coefficient.

ion-selective electrode *or* **ion-selective microelectrode** any electrode (or microelectrode) whose potential responds in a reproducible manner to changes in the concentration (strictly, in the activity) of a specific kind of ion in the solution in which the electrode is immersed and that is insensitive, or essentially so, to changes in the concentrations (strictly, in the activities) of all other kinds of ion in the solution. The electrode has at its surface a thin membrane of electrically conducting material, separating the internal and external solutions, across which an electric potential difference develops. The membrane consists of or contains an electroactive material responsive to the ions to be determined.

iontophoresis **1** the introduction of drugs and other substances through plasma membranes of cultured cells by the transfer of ions brought about by the application of a small electrical potential through electrodes placed on the membrane. **2** *a less common word for* **ionophoresis**.

iota *symbol*: ι (lower case) *or* I (upper case); the ninth letter of the Greek alphabet. For uses *see* **Appendix A**.

IP *or* **i.p.** *abbr. for* intraperitoneal *or* intraperitoneally.

IP_2 *abbr. for* D-*myo*-inositol 3,4-bisphosphate.

IP_3 *abbr. for* D-*myo*-inositol 1,3,4- (or 1,4,5-) triphosphate.

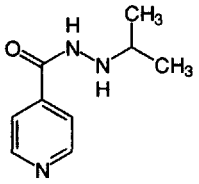
IP_4 *abbr. for* D-*myo*-inositol 1,3,4,5-tetrakisphosphate.

ipecacuanha *or* **ipecac** the dried root of the South American shrub, *Cephaelis ipecacuanha*; it contains the alkaloids **cephaeline** and **emetine**. Ipecacuanha preparations are used as emetics and expectorants.

IPP *abbr. for* Δ^3-isopentenyl pyrophosphate. This compound is now preferably called isopentenyl diphosphate (*abbr.*: IDP).

iPr *symbol for* the isopropyl group, $(CH_3)_2CH-$ (alternative to Pr^i).

iproniazid 1-isonicotinoyl-2-isopropylhydrazine; a derivative of **isoniazid** that is a **monoamine oxidase** inhibitor.



Ips *symbol for* the pipsyl group.

IPTG *abbr. for* isopropyl β-D-thiogalactoside.

IPTS *abbr. for* International Practical Temperature Scale.

Ir *symbol for* iridium.

IR **1** *or* **i.r.** *abbr. for* infrared (radiation). **2** *abbr. for* inverted repeat.

IRE *abbr. for* iron response element.

I_1, I_2 receptors *see* **imidazoline receptor**.

IRG *abbr. for* immunoreactive glucagon.

IRMA *abbr. for* immunoradiometric assay.

iron *symbol*: Fe; a metallic element of group 8 of the IUPAC **periodic table**; proton number 26; natural iron has a relative atomic mass of 55.847 and is a mixture of stable nuclides of nucleon numbers 54 (5.8 atom per cent), 56 (91.7 atom per cent), 57 (2.2 atom per cent), and 58 (0.3 atom per cent). About 12 artificial radioactive nuclides are known; of these, **iron-59** is the one most widely used in biochemistry and molecular biology. Iron is a **transition element** and hence forms ionic salts and numerous complexes in the oxidation states +2, i.e. iron(II) (ferrous iron), or +3, i.e. iron(III) (ferric iron). Iron is one of the most important elements in biology; it is essential in substantial quantities to all cellular organisms from bacteria to mammals, particularly for the synthesis of hemoproteins such as **cytochromes**, **hemoglobins** and related proteins, **myoglobin**, **catalase**, and some **peroxidases**. Important iron-transport proteins include **ferritin** and **transferrin**; iron is taken up into mammalian cells, bound to transferrin, by the **transferrin receptor**. There is no physiological excretory mechanism for iron, but it is lost from females during menstruation.

iron-59 the artificial radioactive nuclide $^{59}_{26}Fe$. It decays to the stable nuclide cobalt-59 with emission of a beta particle (i.e. an electron) in two moderate-energy ranges (0.27 MeV max., 48%, and 0.48 MeV max., 51%) plus gamma radiation of various energies (mainly 1.10 MeV, 56%, and 1.29 MeV, 43%). It has a half-life of 44.5 days.

iron–molybdenum cofactor *abbr.*: FeMo-co; *see* ***nif***, **nitrogenase**.

iron overload a condition of humans in which iron is taken up in excess over a prolonged period. As there is no excretory mechanism for iron, it accumulates in Kupffer cells in the liver as **hemosiderin**, a form of **ferritin** complexed with other proteins and iron. The condition is known as **hemosiderosis**. It is sometimes referred to as **Bantu siderosis**, being very prevalent in these peoples owing to their use of iron cooking pots. It also occurs as a result of repeated blood transfusions, e.g. in treatment for the hemoglobinopathies.

iron response element *or* **iron regulatory element** *abbr.*: IRE; a base sequence in eukaryotic genomes responsible for regulating gene expression of proteins involved in iron metabolism.

ironophore *an alternative name for* **siderochrome**.

iron–sulfur protein *abbr.*: Fe–S protein; any member of a group of proteins to which iron is bound via sulfur-containing ligands (excluding hemoproteins containing iron linked only through axial sulfur ligands). Iron–sulfur proteins are characterized by a relatively low molecular mass and the possession of nonheme bound iron, as well as one or more of the following: (1) acid-labile sulfur; (2) absorption bands between 300 and 600 nm; (3) the capability of transferring electrons at low redox potential; and (4) paramagnetism in one or more oxidation states. They may be classified as **simple** if they contain one or more Fe–S clusters only (*see* **ferredoxin**, **rubredoxin**), and **complex** where additional active groups such as flavin, heme, or another metal are present.

irradiate to subject to or treat with electromagnetic radiation or beams of particles. —**irradiation** *n.*

irreversible competitive antagonist *(in pharmacology)*, an antagonist for which the dissociation rate is so low that antagonist molecules cannot be replaced by increasing the concentration of an agonist for the same receptor.

irreversible process any process occurring in an isothermal system without change of internal energy but with an increase in entropy.

IS *abbr. for* insertion sequence.

islet any small group of cells that is structurally distinct from the surrounding tissue, especially the **islets of Langerhans**.

islet-activating protein *abbr.*: IAP; *a former name for* **pertussis toxin** (so-called because it stimulates release of insulin from the islets of Langerhans).

islets of Langerhans *or (sometimes)* **islands of Langerhans** *or* **pancreatic islets** the numerous small, spherical or oval, highly vascular clusters of endocrine cells that lie scattered throughout the acinar (i.e. exocrine) tissue of the pancreas of gnathostome (i.e. jaw-bearing) vertebrates and are readily distin-

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guishable microscopically from it. The normal adult human pancreas contains about 2 million islets, which together comprise under 2% of its total volume. Islets commonly consist of three main types of cells, all granule-containing: the glucagon-secreting **A cells**; the insulin-secreting **B cells**; and the somatostatin-secreting **D cells**. Some other types of hormone-secreting cells may be present also. [After Paul Langerhans (1847–88), German physician and anatomist, who first described such clusters of cells (1869).]

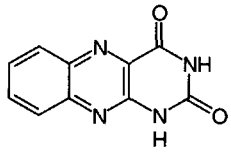
iso+ *or (sometimes before a vowel)* **is+** *comb. form* **1** equal, the same, uniform, homogeneous. *Compare* **allo+** (def. 1), **homo+** (def. 1), **hetero+** (def. 1), **xeno+** (def. 1). **2** *(in immunology and genetics)* **a** in or of some individual or ones that are genetically identical (e.g. **isogenic**). **b** in or of another, genetically differing individual of the same species (e.g. **isoantigen**); **allo+** (def. 2) is now usually preferred. **c** in or of all normal individuals of the same species (e.g. **isotypic**). *Compare* **allo+** (def. 2), **hetero+** (def. 2), **homo+** (def. 2), **xeno+** (def. 2). **3** *(in chemical nomenclature)* **a** signifying isomer of (formerly 'iso' was italicized and often hyphenated). **b** *symbol*: i (as a prefix or superscipt); signifying the isomer of a straight-chain alkane or alkane derivative that differs only in having a terminal $(CH_3)_2CH–$ group (leucine and isoleucine are exceptions). *Compare* **allo+** (def. 3), **nor+** (def. 1). **4** *(in names of certain classes of macromolecules)* signifying irrespective of location or origin, one of two or more structural variants with the same specificity of activity or action (e.g. **isoacceptor tRNA**, **isohormone**; *see also* **isoenzyme**).

ISO *abbr. for* International Standards Organization.

isoacceptor tRNA *or* **isoaccepting tRNA** any of two or more transfer RNA species obtainable from a given organism that can be acylated by the same amino acid; they may differ in their anticodons.

isoagglutinin any antibody formed in one individual that causes agglutination of cells derived from another individual of the same species.

isoalloxazine benzo[*g*]pteridine-2,4(1H,3H)dione; the hypothetical tricyclic parent compound from which is derived any N^{10}-substituted alloxazine. The 7,8-dimethyl derivative is the heterocyclic ring structure in riboflavin and flavin mononucleotide, and one of the heterocyclic ring structures in flavin-adenine dinucleotide.



isoamylase EC 3.2.1.68; *other name*: debranching enzyme; an enzyme that catalyses the hydrolysis of 1,6-α-D-glucosidic branch linkages in glycogen, amylopectin, and their β-limit dextrins. It does not attack pullulan, and is limited in action on α-limit dextrins. Example (precursor) from *Pseudomonas amyloderamosa*: database code ISOA_PSEAY, 771 amino acids (83.24 kDa).

isoantibody any antibody formed in one individual in response to an antigen derived from another individual of the same species.

isoantigen any antigen occurring in an individual that is capable of eliciting an immune response in genetically different individuals of the same species but not in the individual itself.

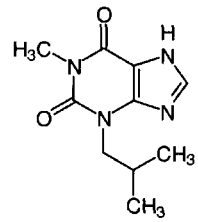
isoasparagine *the trivial name for* the α-amide of aspartic acid, aspartic 1-amide; β-aminosuccinamic acid; 3-amino-3-carbamoylpropanoic acid; $H_2N–CO–CH(NH_2)–CH_2–COOH$; a chiral α-aminoacylamide. L-Isoasparagine (*symbol*: Asp-NH_2) can occur as an N-terminal amidated residue of proteins. *Compare* **asparagine**.

isoasparaginyl the acyl group, $H_2N–CO–CH(NH_2)–CH_2–CO–$, derived from **isoasparagine**. *Compare* **asparaginyl**.

isoaspartyl *the former name for* **β-aspartyl**.

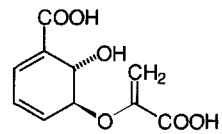
isobar **1** any of two or more nuclides having the same mass number (nucleon number) but different atomic numbers (proton numbers) and hence of differing chemical properties. *See also* **heterotope**. **2** any curve or equation relating quantities measured at the same pressure; any line joining points on a graph or map that have equal pressures. —**isobaric** *adj.*

isobutylmethylxanthine *abbr.*: IBMX; 3-isobutyl-1-methylxanthine; an inhibitor of **cyclic AMP phosphodiesterase**; it raises cyclic AMP levels in cells and tissues.



isocaloric *(of foodstuffs)* having the same **calorific value**.

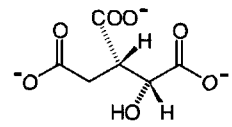
isochorismate 5-[(1-carboxylatoethenyl)oxy]-6-hydroxy-1,3-cyclohexadiene-1-carboxylate; the dianion of isochorismic acid; an isomer of **chorismate** and an important precursor to some compounds in the **shikimate pathway**.



isochorismic acid

isochromosome any chromosome having homologous, genetically identical arms that are mirror images of each other.

isocitrate **1** any of the anionic forms of isocitric acid, 1-hydroxy-1,2,3-propanetricarboxylic acid. (1*R*,2*S*)-1-hydroxypropane-1,2,3-tricarboxylate (*also termed* (2*R*,3*S*)-isocitrate or *threo*-D_s-isocitrate) is an important intermediate in the **tricarboxylic-acid cycle** and the **glyoxylate cycle**. **2** any mixture of free isocitric acid and its ionized forms. **3** any (partial or full) salt or ester of isocitric acid.



(1*R*,2*S*)-1-hydroxypropane-1,2,3-tricarboxylate

isocitrate dehydrogenase 1 **isocitrate dehydrogenase (NAD+)** EC 1.1.1.41; *other names*: isocitric dehydrogenase; β-ketoglutaric-isocitric carboxylase; an enzyme that catalyses the oxidation of isocitrate to 2-oxoglutarate and CO_2, with reduction of NAD^+ to NADH. The isomer of isocitrate involved is (1*R*,2*S*)-1-hydroxypropane-1,2,3-tricarboxylate. Examples from yeast, in which there are two mitochondrial isozymes (precursors): database code IDH1_YEAST, 360 amino acids (39.28 kDa); database code IDH2_YEAST, 369 amino acids (39.69 kDa). In

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mammalian tissues, this enzyme is localized exclusively in the mitochondria. **2 Isocitrate dehydrogenase (NADP$^+$)** (EC 1.1.1.42); an enzyme that is localized in both mitochondria and cytosol.

[isocitrate dehydrogenase (NADP$^+$)] kinase EC 2.7.1.116; *other names*: isocitrate dehydrogenase kinase/phosphatase (*abbr.*: IDH kinase/phosphatase); an enzyme that catalyses the phosphorylation by ATP of isocitrate dehydrogenase (NADP$^+$) with formation of ADP. The phosphorylated protein is the inactive form of the enzyme. Example from *Escherichia coli* in which a bifunctional enzyme contains this and isocitrate dehydrogenase kinase/phosphatase (EC 3.1.3.–) activities: database code ACEK_ECOLI, 578 amino acids (67.51 kDa).

isocitrate lyase EC 4.1.3.1; *systematic name*: isocitrate glyoxalate-lyase; an enzyme, present in the glyoxysomes of seeds, that converts (1*R*,2*S*)-1-hydroxypropane-1,2,3-tricarboxylate (the isomer of isocitrate involved) to succinate and glyoxylate. *See* **glyoxylate cycle**.

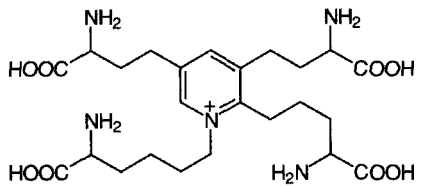
isocratic *(in chemistry)* describing any chromatographic procedure or separation in which the composition of the eluent is maintained constant. *Compare* **gradient elution**.

isocyanate any organic compound containing the univalent group –N=C=O. *Compare* **cyanate**, **isothiocyanate**.

isocyclic see **homocyclic** (def. 1).

isodalt a type of very-high-resolution two-dimensional electrophoresis system for the analysis of small (1–2 mg) samples of complex mixtures of proteins. It employs isoelectric focusing in cylindrical gels in the first dimension, followed by slab-gel electrophoresis in the presence of sodium dodecyl sulfate in the second dimension. Such systems are considered to be capable of resolving mixtures containing 10^4 or more individual proteins within the range 10–200 kDa.

isodesmosine the 2-(4-amino-4-carboxybutyl)-1-(5-amino-5-carboxypentyl)-3,5-bis(3-amino-3-carboxypropyl)pyridinium ion; a tetra(α-amino acid) isolated from hydrolysates of the fibrous protein elastin. *See* **desmosine**.



isodiametric **1** *(of cells)* having similar diameters in all planes. **2** *(of a crystal)* having three equal axes.

isodynamic *(in physics)* having equal force or strength.

isoelectric **1** having the same electrical potential; containing or indicating no potential difference. **2** *(of particles or molecular entities)* having no net electric charge.

isoelectric focusing *or* **electrofocusing** *abbr.*: IEF; a technique in which solutes of different isoelectric points are caused to form stationary bands in an electric field, which is superimposed on a (stable) pH gradient, the pH increasing from the anode to the cathode. In practice the pH gradient is most conveniently formed by electrolysing a solution containing a mixture of **carrier ampholytes** of low molecular mass and slightly differing isoelectric points, each of which will move to its isoelectric region in the electric field and remain there.

isoelectric-focusing electrophoresis a separation technique in which electrophoresis is effected in a gel slab at right angles to a preformed, stationary pH gradient generated by isoelectrically focused carrier ampholytes (*see* **isoelectric focusing**).

isoelectric fractionation any technique for fractionating proteins or other ampholytes using **isoelectric focusing**.

isoelectric pH *an alternative term for* **isoelectric point**.

isoelectric point *or* **isoelectric pH** *abbr.*: IEP *or* i.e.p.; *symbol*: pI; the pH of the solution in which a protein or other ampholyte has zero mobility in an electric field; hence the pH at which the protein or other ampholyte has zero net charge, i.e. no charges or an equal number of positive and negative charges including those due to any extraneous ions bound to the ampholyte molecule. The pH value of the isoelectric point may depend on other ions, except hydrogen and hydroxide ions, present in the solution. *Compare* **isoionic point**.

isoelectric precipitation the precipitation of a protein at its **isoelectric point**, at which proteins are generally least soluble. It is useful in the fractionation of mixtures of proteins.

isoelectronic describing two or more chemical entities having the same number of electrons, especially valence electrons. *Compare* **isosteric**.

isoenergetic taking place at constant energy.

isoenzyme *or* **isozyme** any one of the multiple forms of an enzyme arising from a genetically determined difference in primary structure. Isoenzyme is an operational term to denote any one of a group of enzyme proteins with similar catalytic properties but separable by suitable methods, e.g. by electrophoresis, where knowledge of the nature of the multiplicity may be lacking. If the different enzyme proteins are derived from a common gene, then the term 'multiple forms' rather than 'isoenzymes' should be used. The term embraces **allelozyme** and **multilocus enzyme**. *Compare* **interconvertible enzyme**.

isoflavone 7-*O*-glucosyltransferase EC 2.4.1.170; an enzyme that catalyses the reaction between UDPglucose and isoflavone to form isoflavone 7-*O*-β-D-glucoside and UDP.

isoflurane 2-chloro-2-(difluoromethoxy)-1,1,1-trifluoroethane; a widely used nonflammable volatile anesthetic agent.

isoform any of several multiple forms of the same protein that differ in their primary structure, but retain the same function. They can be produced by different genes or by **alternative splicing** of RNA transcripts from the same gene.

isogeneic *or* **isogenic** describing two or more individuals that possess exactly the same genotype. *See also* **syngeneic**.

isoglucose *see* **high-fructose corn syrup**.

isoglutamine *a trivial name for* the α-amide of glutamic acid; glutamic 1-amide; γ-aminoglutaramic acid; 4-amino-4-carbamoylbutanoic acid; H_2N–CO–CH(NH_2)–[CH_2]$_2$–COOH; a chiral α-amino acylamide. L-Isoglutamine (*symbol*: Glu-NH_2) can occur as an N-terminal amidated residue of proteins. Residues of D-isoglutamine (*symbol*: D-Glu–NH_2) are found in *Staphylococcus aureus* peptidoglycan. *Compare* **glutamine**.

isoglutaminyl the acyl group, H_2N–CO–CH(NH_2)–[CH_2]$_2$–CO–, derived from **isoglutamine**. *Compare* **glutaminyl**.

isoglutamyl *a former name for* **γ-glutamyl**.

isograft *an alternative term for* **syngeneic graft**.

isohormone any of two or more structural variants of a polypeptide hormone that have the same hormonal action and are produced within the same organism, or at least within the same species of organism. —**isohormonal** *adj.*

isohydric describing solutions that have the same hydrogen-ion concentration, hydrogen-ion activity, or pH.

isohydric shift the opposing and counterbalancing changes in hydrogen-ion concentration occurring in peripheral tissues when dioxygen leaves the blood and carbon dioxide enters it. The hydration of CO_2 to H_2CO_3, catalysed by erythrocyte carbonic anhydrase, has a tendency to lower the blood pH. This tendency is counteracted in some degree by the simultaneous deoxygenation of hemoglobin; deoxyhemoglobin binds hydrogen ions more strongly than oxyhemoglobin, thus tending to raise the blood pH.

isoionic pH *an alternative name for* **isoionic point**.

isoionic point *or* **isoionic pH** the pH of a solution of a protein or other ampholyte from which all other ions have been removed, except hydrogen and hydroxide ions formed by dissociation of water or of the protein or ampholyte itself. *Compare* **isoelectric point**.

isoionic solution any solution of a protein or other ampholyte

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that contains no other ions except those arising from dissociation of the solute and the solvent.

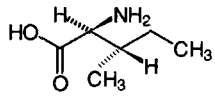
isokinetic gradient any concentration and viscosity gradient used in centrifugation that allows particles (molecules) of the same density to sediment at a constant velocity at all distances from the centre of rotation.

isolate **1** to separate (a pure substance, a cell type, or a sample of a subcellular component) from a mixture or from naturally occurring material and then (usually) to characterize it; to separate and put into pure culture (a particular species or strain of a microorganism) from a mixture, sample, or biological specimen. **2** to remove a viable tissue or organ for the purpose of study or experiment. **3** *(in physics)* to disconnect (part of a circuit), or to prevent interaction between (circuits or components). **4** a group of similar microorganisms, especially a pure culture, obtained by isolation for study, experiment, or as an aid to diagnosis; something isolated. —**isolable** *or* **isolatable** *adj.*; **isolability, isolator** *n.*

isolectin any of two or more molecular forms of lectins, of the same origin, apparently with the same biological properties, and of very similar molecular masses, but of differing electrophoretic mobilities. They may be the products of closely related genes or formed prior to or during isolation. In glycoprotein lectins, their differences may lie in the carbohydrate side chains.

isoleucinate **1** isoleucine anion; the anion, CH_3–CH_2–$CH(CH_3)$–$CH(NH_2)$–COO^-, derived from **isoleucine**. **2** any salt containing isoleucine anion. **3** any ester of isoleucine.

isoleucine *the trivial name for* α-amino-β-methylvaleric acid; (2*R**,3*R**)-2-amino-3-methylpentanoic acid; CH_3–CH_2–$CH(CH_3)$–$CH(NH_2)$–COOH; an α-amino acid with two chiral centres. Because molecules of isoleucine possess a second chiral centre, at C-3, in addition to the chiral centre at C-2 common to all α-amino acids other than glycine, the enantiomers L-isoleucine, (2*S*,3*S*)-2-amino-3-methylpentanoic acid (*symbol*: I *or* Ile), and D-isoleucine, (2*R*,3*R*)-2-amino-3-methylpentanoic acid (*symbol*: D-Ile *or* DIle), are diastereoisomeric with those of **alloisoleucine**, (2*R**,3*S**)-2-amino-3-methylpentanoic acid. L-isoleucine is a coded amino acid found in peptide linkage in proteins; codon: AUA (not in mitochondria of fruit fly, mammals, or yeast), AUC, or AUU. In mammals it is an essential dietary amino acid, and is both glucogenic and ketogenic. D-Isoleucine is not known to occur naturally.



L-isoleucine

isoleucine biosynthesis a pathway that commences with formation of α-aceto-α-hydroxybutyrate (I) from pyruvate and α-ketobutyrate (2-oxobutanoate, formed by removal of ammonia from threonine by serine dehydratase). I is converted via α,β-dihydroxy-β-methylvalerate to α-keto-β-methylvalerate (II). Isoleucine is then formed from II as a result of transamination with glutamate.

isoleucinium isoleucine cation; the cation, CH_3–CH_2–$CH(CH_3)$–$CH(NH_3^+)$–COOH, derived from **isoleucine**.

isoleucino the alkylamino group, CH_3–CH_2–$CH(CH_3)$–$CH(COOH)$–NH–, derived from **isoleucine**.

isoleucyl the acyl group, CH_3–CH_2–$CH(CH_3)$–$CH(NH_2)$–CO–, derived from **isoleucine**.

isoliquivitigenin *see* **chalcone**.

isolog *the US spelling of* **isologue**.

isologous **1** of, relating to, or being two or more closely related chemical compounds in a series whose successive members differ in composition in a regular manner, other than by a difference of one methylene group. The term is now applied especially to compounds that have different atoms of the same valency at one or more positions in the molecule but are otherwise structurally identical, e.g. methionine and selenomethionine. **2** *an alternative term for* **isogeneic**.

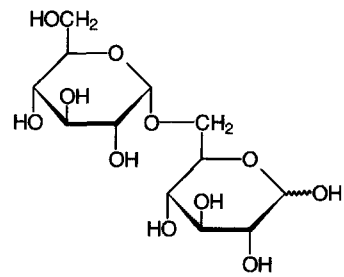
isologous association *or* **isologous binding** any association between two identical protein subunits (i.e. **protomers**) in which the **domain of bonding** is made up of two identical **binding sets**.

isologue *or (US)* **isolog** any of two or more **isologous** (def. 1) compounds.

isology the state or condition of being **isologous** (def. 1); chemical kinship among molecules or compounds.

isomaltase EC 3.2.1.10; *recommended name*: oligo-1,6-glucosidase; *systematic name*: dextrin 6-α-D-glucanohydrolase. An enzyme that hydrolyses 1,6-α-D-glucosidic bonds in dextrins and isomaltose produced after α-amylase degradation of starch and glycogen. The enzyme from intestinal mucosa also catalyses the reaction of EC 3.2.1.48 (*see* **sucrase**). Example from *Bacillus* sp.: database code O16G_BACSP, 508 amino acids (59.78 kDa).

isomaltose the disaccharide 6-*O*-α-D-glucopyranosyl-D-glucose; it exists as the branching unit in **amylopectin**, **glycogen**, and some bacterial **dextrans**. *Compare* **maltose**.



isomaltulose the disaccharide 6-*O*-α-D-glucopyranosyl-D-fructofuranose.

isomer **1** *(in chemistry)* **molecular isomer** any of two or more compounds that have identical molecular formulas but differ in the nature of bonding of their atoms (**constitutional isomers**) or in the arrangement of their atoms in space (**stereoisomers**). **2** *(in physics)* **nuclear isomer** any of two or more nuclides that have the same proton number and the same mass (nucleon) number but different energy states.

isomerase any enzyme of EC class 5 that catalyses geometric or structural changes within one molecule. According to the type of isomeric change they catalyse, they may be called racemases or epimerases (EC subclass 5.1); *cis–trans*-isomerases (EC subclass 5.2); intramolecular oxidoreductases (EC subclass 5.3); intramolecular transferases (mutases) (EC subclass 5.4); or intramolecular lyases (EC subclass 5.5); other isomerases are placed in EC subclass 5.99.

isomeric of or pertaining to an **isomer**; pertaining to the phenomenon of, or displaying, **isomerism**.

isomeric state any of the states of an atomic nucleus having a different energy and observable half-life from those of other states of the same nucleus; the condition of being an **isomer** (def. 2).

isomeric transition *abbr.*: IT; the change of one nuclear isomer (*see* **isomer** (def. 2)) into another without change in either proton number (atomic number) or nucleon number (mass number), energy being lost in the form of gamma radiation; e.g. the decay of the metastable nuclide technetium-99m (half-life 6 h) to the unstable nuclide technetium-99 (half-life 2.1 × 10^5 years), which in turn decays to ruthenium-99 with emission of an electron.

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isomerism the phenomenon of the existence of **isomers** in general, or the occurrence of molecular or nuclear isomers in a particular instance.

isomerization *or* **isomerisation** the act of changing or the process of change of one molecular isomer into another one. —**isomerize** *or* **isomerise** *vb.*

isometric **1** having identical dimensions. **2** *(in physiology)* of or pertaining to a contraction of a muscle that does not cause shortening of the muscle. **3** *(in crystallography)* having three mutually perpendicular axes of equal length; cubic.

isomorph a substance or organism that is **isomorphic** (def. 1) to another substance or organism.

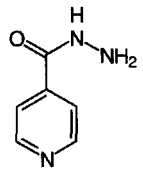
isomorphic **1** *or* **isomorphous** of identical or similar form, shape, or structure. **2** describing a type of alternation of generations in which morphologically identical generations occur in both diploid and haploid phases. It occurs mainly in algae. *Compare* **heteromorphic**.

isomorphism **1** *(in biology)* similarity of form in organisms of different ancestry. **2** *(in chemistry)* similarity of crystalline form and structure between substances of similar composition or substances that can form a more or less continuous series of solid solutions.

isomorphous **1** *an alternative term for* **isomorphic** (def. 1). **2** displaying **isomorphism** (esp. def. 2).

isomorphous replacement method a method used to solve the phase problem in **X-ray diffraction** analysis of macromolecular structures. It involves combining one or more **heavy atoms** (def. 2) (which are strong scatterers) in a specific manner with the macromolecule in question and investigating their effects on the diffraction pattern. The heavy atom must not modify either the conformation or the crystal form of the macromolecule, i.e. the replacement must be isomorphous.

isoniazid 4-pyridinecarboxylic acid hydrazide; an antitubercular drug that may act by inhibiting the synthesis of the mycolic acids that are vital for the construction of the cell wall of the pathogen, *Mycobacterium tuberculosis*. Like related hydrazides it is highly hepatotoxic and no longer used. Its euphoric side effects led to the discovery of monoamine oxidase inhibitors.

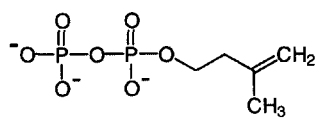


isoosmotic *a variant spelling of* **isosmotic**.

isopartitive *(in chromatography)* describing two or more solvents that bring about similar partitions of a given substance between the solvent and the stationary phase and hence result in R_f values that are the same or nearly so.

isopentenyl *the trivial name for* 3-methylbut-3-enyl, $CH_2{=}C(CH_3){-}CH_2{-}CH_2{-}$, the alkenyl group formally derived from isopentenyl alcohol (i.e. 3-methylbut-3-en-1-ol) by loss of its hydroxyl group. *Compare* **prenyl**.

isopentenyl diphosphate *abbr.*: IDP; *formerly called* Δ^3-isopentenyl pyrophosphate (*abbr.*: IPP); an isomer of dimethylallyl diphosphate and the key precursor of all **isoprenoids** (def. 2). *See also* **dimethylallyl*trans*transferase**, **isopentenyl-diphosphate Δ-isomerase**, **isoprene rule**.



isopentenyl-diphosphate Δ-isomerase EC 5.3.3.2; *systematic name*: isopentenyl diphosphate Δ^3–Δ^2-isomerase; *other name*: IPP isomerase. An enzyme in the pathway for the synthesis of cholesterol, terpenes, and prenyl groups; it catalyses the reversible reaction:

isopentenyl diphosphate = dimethylallyl diphosphate.

Example from *Saccharomyces cerevisiae*: database code IPPI_YEAST, 287 amino acids (33.18 kDa).

isopeptidase any peptidase catalysing the cleavage of an **isopeptide bond**.

isopeptide bond any peptide bond other than one that is a **eupeptide bond**, i.e. any amide bond formed between a carboxyl group of one amino-acid molecule or residue and an amino group of another where either group occupies a position other than α (or both do so). Examples include peptide bonds formed from the β-carboxyl group of aspartic acid, the γ-carboxyl group of glutamate from the ε-amino group of lysine, and from either the carboxyl group or the amino group of β-alanine.

isopiestic of, pertaining to, or characterized by equal pressures.

isopiestic vapour pressure method a method for the determination of the activity of water in a solution of a nonvolatile solute. The solution in question is equilibrated with a reference solution containing a nonvolatile solute for which the activity of water at different solute concentrations has been determined with high precision. The two solutions are placed in an enclosure at constant temperature until their vapour pressures are equal, i.e. the activity of water in both solutions is equal. They are then analysed for their solute contents, from which the activity of water in both of them can be calculated.

isoprenaline *an alternative name for* **isoproterenol**.

isoprene 2-methylbuta-1,3-diene; $CH_2{=}C(CH_3){-}CH{=}CH_2$; a liquid hydrocarbon hemiterpene isolated from products of the pyrolysis of natural rubber, turpentine, etc., and widespread in plants although generally found only in extremely small amounts.

isoprene residue the branched-chain bivalent group, 3-methyl-2-butenylene; 3-methylbut-2-en-1,4-diyl; $-CH_2{-}C(CH_3){=}CH{-}CH_2-$. It is formally derived by bond rearrangement from **isoprene** and constitutes the repeating unit of the molecular structures of prenols and many other isoprenoids.

isoprene rule a rule, formulated by Wallach in 1887, that stated that many natural products are built up from isoprene carbon skeletons. It was modified to the **biogenetic isoprene rule** by **Ružička**, who proposed that all terpenoids, steroids, etc. are synthesized from a precursor called 'active isoprene'. This precursor is now known to be **isopentenyl diphosphate**.

isoprene unit *(in an isoprenoid)* an **isoprene residue** or any branched five-carbon-atom moiety formally derived from an isoprene residue by chemical modification, e.g. by hydrogenation, hydroxylation, etc. It represents isopentenyl alcohol (i.e. 3-methylbut-3-en-1-ol), the diphosphate of which is the universal biogenetic precursor of isoprenoids.

isoprenoid **1** of, pertaining to, or being **isoprene** and its chemical relatives; having a molecular structure composed of, containing, or derived from linked **isoprene residues**. **2** any isoprenoid compound. Isoprenoids comprise a large and varied family of natural products, including carotenoids, phytol, prenols, rubber, steroids, terpenoids, and tocopherols. Many substances contain both isoprenoid and nonisoprenoid components, e.g. the vitamins K.

isoprenyltransferase any of the enzymes within subclass EC 2.5.1, existing as α–β heterodimers, that add C_{15} or C_{20} carbon chains by **prenylation** near the carboxyl terminus of proteins. Examples include the nuclear lamins and Ras.

isopropyl *symbol*: iPr *or* Pr^i; the alkyl group $(CH_3)_2CH-$, derived from propane. *Compare* **propyl**.

isopropylmalate either of the isomeric substances 2-isopropylmalate (i.e. 3-carboxy-3-hydroxy-4-methylpentanoate) or 3-

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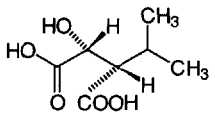
isopropylmalate (i.e. 3-carboxy-2-hydroxy-4-methylpentanoate); they are enzymatically interconvertible intermediates in the biosynthesis of leucine in plants. *See also* **3-isopropylmalate dehydratase**.



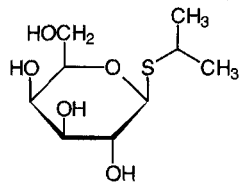
(2*R*,3*S*)-3-isopropylmalic acid

3-isopropylmalate dehydratase EC 4.2.1.33; *systematic name*: 3-isopropylmalate hydro-lyase; an enzyme that catalyses the isomerization of 3-isopropylmalate to 2-isopropylmalate, by dehydration to 2-isopropylmaleate and rehydration to generate the isomer, in the pathway of L-leucine biosynthesis in plants. *See* **leucine and valine biosynthesis**.

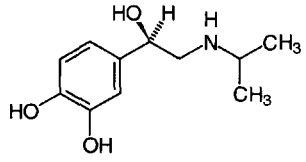
3-isopropylmalate dehydrogenase EC 1.1.1.85; *systematic name*: 3-carboxy-2-hydroxy-4-methylpentanoate:NAD^+ oxidoreductase; an enzyme that catalyses the oxidation of 3-**isopropylmalate** by NAD^+ (followed by loss of CO_2) to 4-methyl-2-oxopentanoate, in the pathway of L-leucine biosynthesis in plants. *See* **leucine and valine biosynthesis**.

2-isopropylmalate synthase EC 4.1.3.12; *systematic name*: 3-carboxy-3-hydroxy-4-methylpentanoate 3-methyl-2-oxobutanoate-lyase (CoA-acetylating); an enzyme that condenses acetyl-CoA with 3-methyl-2-oxobutanoate to form 2-isopropylmalate, in the pathway of L-leucine biosynthesis in plants. *See* **leucine and valine biosynthesis**.

isopropyl β-thiogalactoside *abbr.*: IPTG; isopropyl β-D-1-thiogalactopyranoside; an inducer of β-galactosidase in bacteria; it also induces the *lac* operon by binding and inactivating the *lac* repressor. It is used in cloning techniques to enhance expression of DNA cloned into vectors containing the *lac* operon.



isoproterenol *or* **isoprenaline** 3,4-dihydroxy-α-[(isopropylamino)methyl]benzyl alcohol; the synthetic isopropyl analogue of epinephrine. It is a selective agonist of β adrenoceptors, but does not discriminate between β_1 and β_2 subtypes.



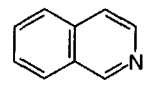
isoproterenol

isopycnic of, pertaining to, or characterized by equal densities.

isopycnic banding the formation during **isopycnic centrifugation** of one or more bands composed of molecules that have the same density as that of the solvent at that position in the gradient; the process of separating or purifying substances by forming such bands.

isopycnic centrifugation *or* **band centrifugation** *or* **density-gradient centrifugation** *or* **density-gradient sedimentation equilibrium** a separation technique in which macromolecules are subjected to a centrifugal field in a solvent containing a density gradient. The macromolecules will sediment or float and arrange themselves in bands (isopycnic bands) in the column of solvent where the density of the solvent is the same as that of the particular macromolecule. *Compare* **isokinetic gradient**.

isoquinoline 2-benzazine; benzo[*c*]pyridine; a bicyclic, aromatic, nitrogen-containing compound. Many alkaloids contain an isoquinoline ring system.



isoquinolinesulfonylmethylpiperazine *see* **H7**.

isosbestic point any wavelength at which the molar **absorption coefficients** of two or more particular chemical species are equal, i.e. their absorption spectra intersect. All mixtures (or solutions) of two or more such species, having the same total concentration, will then exhibit absorption spectra that pass through the isosbestic point, provided the species do not interact.

isoschizomer any of two or more restriction endonucleases from different sources that recognize the same sequence in a DNA molecule and display identical specificity of cleavage within that sequence. The term is sometimes extended to include those enzymes that cleave at different sites within the sequence recognized, or that respond to methyl groups on different bases in the sequence. Examples are *Msp*I and *Hpa*II, both of which cleave the unmethylated sequence CCGG. —**isoschizomeric** *adj.*

isosemantic substitution the incorporation of an amino-acid residue into its normal position in a polypeptide chain in response to a mutated but synonymous codon.

isosmotic *or* **isoosmotic** *(of two or more solutions)* having equal osmotic pressure; having the same osmotic pressure as another solution. *See also* **isotonic** (def. 2).

isostere *or* **isoster** any of two or more **isosteric** chemical species.

isosteric *(of two or more chemical species)* having the same, or similar, shape and size, e.g. L-threonine and L-valine; having the same number of valence electrons arranged in a similar manner. *Compare* **isoelectronic**. —**isosterism** *n.*

isotachophoresis *or* **isotachoelectrophoresis** *or* **displacement electrophoresis** a method for separating ion species in which all ions under observation are given the same migration velocity; moreover, they all have the same sign and a common counterion. The sample ions are introduced as a zone between a leading electrolyte, whose ions have a higher mobility than any of the sample ions, and a terminating electrolyte, whose ions have a lower mobility than any of the sample ions.

isotactic of, relating to, or having stereochemical regularity in the repeating units of a polymer. *Compare* **syndyotactic**.

isotherm *or* **isothermal** any line on a graph, or diagram, that connects points of equal temperature.

isothermal **1** *(of a process or reaction)* occurring at constant temperature. **2** of or pertaining to an isotherm. **3** *an alternative name for* isotherm.

isothiocyanate any organic compound containing the monovalent group –N=C=S. *Compare* **thiocyanate**.

isotocin *or (formerly)* **isotocine** [Ser^4,Ile^8]oxytocin; the somewhat less potent structural variant of **oxytocin**. It is present in many bony fish in place of oxytocin, hence it is sometimes known as **ichthyotocin**. *See also* **mesotocin**.

isotope any of two or more nuclides having the same number

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of neutrons but, usually, different numbers of protons and therefore differing in atomic number.

isotonic **1** of, or having the same tension; used especially of muscular contraction occurring in the absence of significant resistance and accompanied by marked shortening of the muscle fibres. *Compare* **isometric** (def. 2). **2** having the same osmotic pressure as some particular solution, especially one in a cell or body fluid; **isosmotic**. *Compare* **hypertonic**, **hypotonic**. **3** of, relating to, or being an **isotone** or isotones.

isotonically under **isotonic** (def. 1) conditions.

isotonicity the state or quality of being **isotonic** (def. 2); the degree of osmotic pressure.

isotope any of two or more **nuclides** that have the same **proton number**, i.e. that are nuclides of the same chemical element and thus display qualitatively the same chemical properties (for quantitative differences, *see* **isotope effect**). Isotopes with a given proton number usually have different **nucleon numbers** and thus characteristically usually have different relative atomic masses. In some instances, however, two isotopes of an element are isomeric, i.e. they have the same nucleon number (and hence the same relative atomic mass) but differ instead in their nuclear energy levels, the isotope with the higher level being **metastable** (def. 3). For the majority of elements, isotopes occur naturally and at more or less constant relative abundances; additional isotopes can be produced artificially. In general, any given element possesses both stable and unstable isotopes, although there are no stable ones for elements of high proton number; conversely, the naturally occurring isotopes of elements of lower proton number are, with a few exceptions, all stable. Metastable and unstable isotopes undergo radiative decay and are collectively termed radioactive isotopes, or radioisotopes. (*Note*: In common parlance the term isotope is often used loosely as a synonym of nuclide irrespective of its proton number.) *Compare* **heterotope**, **isobar**, **isotone**. —**isotopic**, *adj.*

isotope abundance the number of atoms of a particular isotope in a mixture of the isotopes of an element in a sample, expressed as a percentage of all the atoms of that element in the sample. *Compare* **isotope ratio**.

isotope dilution analysis an accurate method for measuring the concentration of an element, or a compound of that element, in a system by adding a known amount of a different isotope, or a labelled compound, and then measuring its concentration in a sample withdrawn from the system after mixing.

isotope effect any variation in some chemical, physicochemical, or biochemical property of a molecular entity that is detectable on isotopic substitution of an atom or atoms of the entity, e.g. variation in reaction rate, in chromatographic mobility, or in binding to macromolecules. For a given pair of isotopes, 'light' and 'heavy', the effect may be expressed quantitatively either (in the **kinetic isotope effect**) as the ratio of the rate constants, k_{light}/k_{heavy}, or (in the **equilibrium isotope effect**) as the ratio of the equilibrium constants, K_{light}/K_{heavy}, for two chemical reactions that differ only in the isotopic composition of one or more of their otherwise chemically identical components. The magnitude of the effect depends on the relative difference in atomic mass of the isotopes in question; thus it is the greatest by far for isotopes of hydrogen.

isotope exchange any chemical reaction in which the reactants and products are chemically identical but of different isotopic composition. In such a reaction the isotope distribution tends towards equilibrium.

isotope farming *an informal term sometimes used to describe* biological techniques for the large-scale preparation, usually for sale, of radioisotope-labelled biochemicals, especially when a number of such compounds are obtainable in the same operation, e.g. the simultaneous preparation of a number of ^{14}C-labelled compounds from $^{14}CO_2$ by photosynthesis in whole leaves or whole plants.

isotope ratio *or* **isotopic ratio** the ratio between the numbers of atoms of any two isotopes of a given element in a particular preparation, sample, or substance. *Compare* **isotope abundance**.

isotope-ratio mass spectrometer a ***mass spectrometer*** designed specifically for the determination of **isotope ratios**.

isotopic **1** of, relating to, or being an **isotope** or isotopes. **2** being or containing a less common or artificial isotope, especially as a label or tracer. **3** *(especially of techniques)* using or depending on isotopes. —**isotopically** *adv.*

isotopy the phenomenon of the existence of isotopes in general; or the fact or condition of being isotopic in a particular instance.

isotropic *or* **isotropous** **1** *(in physics)*: exhibiting uniform properties when measured along axes in all directions. *Compare* **anisotropic**. **2** *(in biology)* not having predetermined axes of growth. —**isotropically** *adv.*; **isotropy** *or* **isotropism** *n.*

isotropic band *or* **I-band** *see* **sarcomere**.

isotropic motion the random tumbling of a chemical species about its three axes.

isotropous *an alternative word for* **isotropic**.

isotypic specificity any antigenic specificity that is the same in a given protein in all normal individuals of the same animal species. For example anti-rabbit gamma globulins prepared in another animal species do not distinguish between gamma globulins from different rabbits.

isotypic variation structural variability of any one antigen that is common to all members of the same species.

isovaleric acidemia a hereditary metabolic disease of humans, due to defects in **isovaleryl-CoA dehydrogenase** i.e. Leu→Pro at position 13 and Gly→Val at position 170 (of the mature enzyme). It is of variable severity.

isovaleryl-CoA dehydrogenase *abbr.*: IVD; EC 1.3.99.10; a flavoprotein enzyme of the pathway for degradation of valine. It catalyses the oxidation of 3-methylbutanoyl-CoA to 3-methylbut-2-enoyl-CoA. The flavin is FAD. Example (precursor) from human: database code IVD_HUMAN, 423 amino acids (46.27 kDa).

isozyme *an alternative word for* **isoenzyme**.

isozymogen any precursor of an isozyme.

IT *abbr. for* isometric transition.

itaconate methylenesuccinate; methylenebutanedioate; the dianion $^{-}OOC–CH_2–C(=CH_2)–COO^{-}$; a constitutional isomer of **citraconate**. It is a metabolite of strains of *Aspergillus terreus*, which can yield it in large amounts by decarboxylation of *cis*-aconitate. It is a comparatively reactive compound, with properties useful in the manufacture of synthetic resins and plastics.

iteron any sequence of nucleotides in the duplex DNA of certain lambdoid phages that is reiterated several times with only minor changes. These repeated sequences, of 13–19 base pairs, are usually separated by short spacer sequences, each having internal dyad symmetry.

+itis *suffix forming nouns* denoting inflammation of the (specified) organ, tissue, etc.

ITP *abbr. for* **1** inosine (5′-)triphosphate. **2** isotachophoresis.

itraconazole a complex derivative of triazole, useful as an antimycotic. It inhibits cytochrome P450-dependent enzymes, thereby impairing the synthesis of ergosterol.

+ity *suffix forming nouns* meaning a property of a substance; e.g. absorptivity, density, solubility.

IU *abbr. for* International Unit *(preferred alternative to* **i.u.** *or* **u***)*.

IUB *abbr. for* International Union of Biochemistry; renamed (1992) International Union of Biochemistry and Molecular Biology (IUBMB).

IUBMB *abbr. for* International Union of Biochemistry and Molecular Biology. *See* **Appendix C**.

IUdR *or* **IUDR** *abbr. for* 5-iododeoxyuridine (IdUrd preferred).

IUPAB *abbr. for* International Union of Pure and Applied Biophysics.

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IUPAC *abbr. for* International Union of Pure and Applied Chemistry.

iupaciubin alanyl-lysyl-glutamyl-tyrosyl-leucine; a pentapeptide containing one residue each of the five main types of amino acid found in peptides and proteins, i.e. small neutral, basic, acidic, aromatic, and lipophilic. It exists only on paper and was designed as a model to illustrate nomenclature recommendations relating to the modification of named peptides. Its name symbolizes the cooperation between IUPAC and IUB.

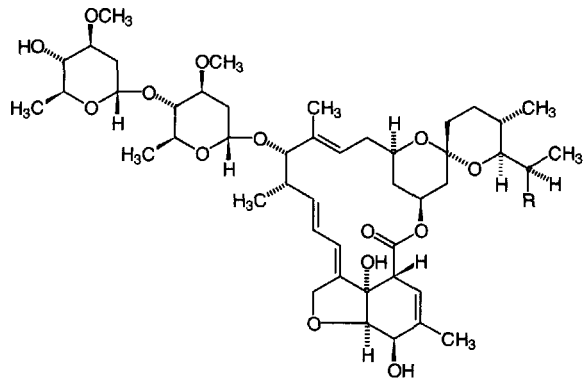
IUPAP *abbr. for* International Union of Pure and Applied Physics.

IV *or* **i.v.** *abbr. for* intravenous or intravenously.

IVD *abbr. for* isovaleryl-CoA dehydrogenase.

ivermectin 22,23-dihydroabamectin; 22,23-dihydroavermectin B_1; a semisynthetic material derived from **abamectin** and used as an anthelmintic in both clinical and veterinary practice, especially against onchocerciasis. It is used extensively as a once-a-month pill against heartworm in dogs.

iVI *symbol for* the isovaleryl group, $(CH_3)_2CH–CH_2–CO–$ (alternative to VI^i).



component B_{1a}, R = C_2H_5
component B_{1b}, R = CH_3

ivermectin

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Jj

j *symbol for* electric current density (alternative to *J*).

J *symbol for* **1** joule. **2** J chain (of an immunoglobulin).

J *symbol for* **1** coupling constant. **2** flux (def. 2). **3** electric current density (preferred alternative to *j*).

jack bean **1** an annual tropical American leguminous plant, *Canavalia ensiformis*, grown in the USA for forage. **2** the seed of this plant. It is the source of the globulin **canavalin**, the toxic amino acid L-canavanine, the lectin **concanavalin A**, and the enzyme **urease**.

Jacob, François (1920–), French molecular biologist notable, *inter alia*, for coining the term **allosteric**, for postulating the existence of **messenger RNA**, and for studies of genetic regulatory mechanisms in protein synthesis (all with J. L. Monod); Nobel Laureate in Physiology or Medicine (1965) jointly with J. L. Monod and A. M. Lwoff 'for their discoveries concerning genetic control of enzyme and virus synthesis'.

Jacob–Monod model a model of genetic regulation of protein synthesis in prokaryotes whereby the structural genes that determine the organization of the proteins are controlled by other regions of DNA upstream from the structural genes. The latter consist of a regulator gene and a **control site**, which comprises the **promotor** (*p*) and **operator** (*o*). The regulator gene produces a **repressor** (*r*), which interacts with the operator. The operator and its associated genes are called an **operon**. The structural genes are transcribed into a single mRNA coding for the several proteins. An mRNA coding for more than one protein is known as a **polygenic** or **polycistronic** transcript. The first example was the ***lac* operon** but the model has been used to elucidate many other such phenomena, e.g. the **tryptophan** and **arabinose** operons. The repressor can be either inactivated (**induction**) or activated (**repression**) by specific metabolites. While the model has been helpful in explaining the mode of expression of genes in eukaryotes, operons have not been described in them. [After F. **Jacob** and J. **Monod**.]

Jamaican vomiting sickness a syndrome of sickness, vomiting, and poisoning of the nervous system, associated with profound hypoglycemia, induced by consumption of the unripe fruit of the **ackee**, the toxic principle of which is **hypoglycin**.

jaundice *or* **icterus** a yellowing of the skin and/or of the whites of the eyes indicating an excess of bilirubin in the blood. Jaundice may be classified into three types depending on cause: **obstructive jaundice**, in which the passage of bile from the liver to the intestine is obstructed; **hepatocellular jaundice**, in which there is disease and/or inflammation of liver cells thus diminishing their ability to secrete bile pigments into the bile passages; and **hemolytic jaundice**, in which there is an excessive breakdown of erythrocytes in the body and hence an excess of bile pigments.

JCBN *abbr. for* (IUPAC–IUB *or* IUPAC–IUBMB) Joint Commission on Biochemical Nomenclature. *See also* **CBN**.

J chain *or* **J piece** *abbr. for* joining chain *or* joining piece; a 15 kDa, cysteine-rich polypeptide chain occurring in **immunoglobulin A** (IgA) and **immunoglobulin M** (IgM) molecules. It is concerned in cross-linking the monomeric immunoglobulin moieties to form a dimer or pentamer in IgA and IgM, respectively. It is not to be confused with the J segment of an immunoglobulin gene (*see* **joining gene**). Example from human: database code IGJ_HUMAN, 137 amino acids (15.58 kDa).

jejunum the part of the small intestine of mammals between the duodenum and the ileum. —**jejunal** *adj.*

jelly roll a motif in protein structure consisting of two antiparallel β sheets placed one above the other to form a sandwich structure. The polypeptide chain follows a route in which successive β strands alternate between the two sheets. If the β strands are numbered β_1, β_2, etc. and the β sheets numbered in parentheses, as (1), (2), etc. the structure of the motif can be represented as loop-β_1(1)-loop-β_2(2)-loop-β_3(1)-loop-β_4(2)-loop-β_5(1), etc. The jelly-roll motif was first observed in viral coat proteins but has since been found in other proteins, the first of these to be determined being tumour necrosis factor.

Jerne, Niels Kaj (1911–94), Danish microbiologist and immunologist distinguished for his pioneering theories of antibody generation; Nobel Laureate in Physiology or Medicine (1984) jointly with G. J. F. Köhler and C. Milstein 'for theories concerning the specificity in development and control of the immune system and the discovery of the principle for production of monoclonal antibodies'.

Jerne's theory of immunity *an alternative name for* **natural-selection theory of immunity**.

J gene *abbr. for* joining gene.

Job's method *an alternative name for* **continuous variation**.

Johnston–Ogston effect a phenomenon occurring in sedimentation velocity experiments when two or more solutes are present in a mixture and their sedimentation coefficients are mutually concentration-dependent. It follows that the sedimentation coefficient of the more slowly sedimenting component is less in the plateau region containing both species than it is in the plateau region between the boundaries, resulting in a higher concentration of the more slowly moving component in the plateau region between the boundaries. As a consequence, the apparent concentration of the faster moving species, based on the concentration difference between the two plateaus, is too low, while the apparent concentration of the more slowly moving species is too high. [After Alexander George Ogston (1911–96) and Joseph Percy Johnston (1923–76), British biochemists.]

joinase *or* **joining enzyme** *a former name for* DNA ligase (ATP) and DNA ligase (NAD^+). *See* **DNA ligase**.

joining gene *or* **J segment** *abbr.*: J gene; any member of a group of approximately five germ-line genes concerned in coding for **immunoglobulin** synthesis. The J genes code for the fourth framework region of both light and heavy immunoglobulin chains and for part of the third hypervariable region of the light chain. *Compare* **J chain**.

joining peptide an acidic 18-residue peptide situated between γ_3-MSH and ACTH in **proopiomelanocortin**.

Joliot, Jean Frédéric (1900–58), latterly adopting the surname Joliot-Curie, French nuclear physicist noted particularly for the production, in collaboration with his wife, I. Joliot-Curie, of the first artificial radioactive nuclides by bombarding stable elements, e.g. boron or aluminium, with fast alpha-particles; Nobel Laureate in Chemistry (1935) jointly with I. Joliot-Curie 'in recognition of their synthesis of new radioactive elements'.

Joliot-Curie **1 Irène Joliot-Curie** (1897–1956), daughter of M. and P. Curie (*see* **Curie**), French nuclear physicist noted particularly for the production, in collaboration with her husband, J. F. Joliot, of the first artificial radioactive nuclides; Nobel Laureate in Chemistry (1935) jointly with J. F. **Joliot**. **2** surname latterly adopted by J. F. Joliot.

Jones–Mote sensitivity a weak, delayed-type hypersensitivity of the skin seen on challenge a few days after priming with soluble protein in aqueous solution or in incomplete Freund's adjuvant. The cells infiltrating the lesion characteristically include a high proportion of basophils.

joule *symbol*: J; the SI derived unit of energy, work, or heat, equal to a force of one newton acting over a distance of one metre; i.e. 1 J = 1 N m = 1 W s. The joule is equivalent to 10^7 ergs and is the energy dissipated by one watt in one second. [After James Prescott Joule (1818–89), British physicist.]

J piece *an alternative name for* **J chain**.

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J segment *an alternative name for* **joining gene**.

jumping gene *an informal term for* **transposon**.

JUN a gene family encoding nuclear transcription factors; v-*jun* is the oncogene from avian sarcoma virus ASV17 (named from *junana*, Japanese for seventeen). *JUN* encodes transcription factor AP1; it belongs to the *FOS*/*JUN* family, and is rapidly and transiently expressed on stimulation of cells by mitogens. The product, Jun, forms heterodimers with Fos, and these, together with Jun homodimers, bind to the AP1 consensus site. Jun is a leucine zipper protein, which also contains basic sequences essential for DNA binding. In resting cells Jun is phosphorylated on four serines and one threonine; removal of one or more of these phosphates leads to increased binding to the AP1 promoter site. Jun has five motifs. Database code TAP1_HUMAN, 331 amino acids (35.63 kDa).

junction potential *see* **liquid-junction potential**.

'junk' amino acid any **noncontributing amino acid**.

'junk' DNA *see* **selfish DNA hypothesis**.

juvenile hormone any insect hormone, produced in the corpora allata glands, that functions to keep the insect in the larval (juvenile) stage. At least three are known; all are derivatives of farnesoic acid. They have potential as insect control agents.

juvenile-hormone esterase *see* **methylesterase**.

juxtacrine stimulation a mode of intercellular communication established by the binding of a membrane-anchored growth factor on one cell to its receptor on an adjacent cell, e.g. in the case of pro-transforming growth factor-α (*see* **transforming growth factor**). Unlike endocrine, paracrine, or autocrine modes there is no diffusible factor.

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Kk

k *symbol for* kilo+ (SI prefix denoting 10^3).

k *symbol for* **1** rate constant; the various associated terms are distinguished by subscripts and/or superscripts (see individual entries below). **2** **Boltzmann constant**. *See also* ***k*(*T*)**.

$\tilde{k}$ *symbol for* pH-independent value of the rate constant k.

k_0 *symbol for* catalytic constant (of an enzyme); alternative to k_{cat}.

k_A, k_B *symbols for* the specificity constants of substances A and B.

k_{app} *symbol for* the apparent value of the rate constant k.

k_{cat} *symbol for* catalytic constant (of an enzyme); alternative to k_0.

k_i, k_{-i} *symbols for* the forward and reverse rate constants, respectively, for the ith step in an enzyme reaction.

k_{ij} *symbol for* the rate constant for the step from E_i to E_j in an enzyme reaction.

K *symbol for* **1** potassium. **2** kelvin. **3** a residue of the α-amino acid L-lysine (alternative to Lys). **4** a residue of an incompletely specified base in a nucleic-acid sequence that may be guanine, or either thymine (in DNA) or uracil (in RNA). **5** phylloquinone. **6** *(in computing)* indicating multiplied by 1024 (= 2^{10}).

K *symbol for* **1** (thermodynamic) equilibrium constant (of a chemical reaction); the various associated terms are distinguished by subscripts and/or superscripts (see individual entries below). **2** kinetic energy. **3** kerma (kinetic energy released in matter). **4** luminous efficacy.

K' *symbol for* apparent (concentration) equilibrium constant.

K^o *or* $K^{\ominus}$ *symbol for* standard equilibrium constant.

K_1, K_2, ... K_n *symbols for* the first, second, ... nth equilibrium (dissociation or association) constants, respectively, of the same substance.

K_a, K'_a *symbols for* the thermodynamic and apparent **acid dissociation constants**, respectively.

K_A *symbol for* activator constant.

K_b, K'_b *symbols for* the thermodynamic and apparent **basic dissociation constants**, respectively.

K_c *symbol for* equilibrium constant with respect to concentration (concentration equilibrium constant).

K_i *symbol for* inhibition constant (inhibition type unspecified); the reactant to which it relates may be indicated by an appropriate subscript, e.g. K_{iA}.

K_{ic} *symbol for* competitive inhibition constant.

K_{iu} *symbol for* uncompetitive inhibition constant.

K_m *symbol for* Michaelis constant (*also called* **Michaelis concentration** *or*, *more appropriately* **Michaelis–Menten constant**); the reactant to which it relates may be indicated by an appropriate subscript, e.g. K_{mA}.

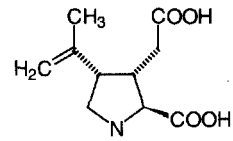
K_s *symbol for* substrate dissociation constant; the reactant to which it relates may be indicated by an appropriate subscript, e.g. K_{sA}.

K_s' *symbol for* salting out constant.

K_w *symbol for* the ion product of water.

kainate receptor a type of excitatory amino-acid receptor characterized by its specific agonist ligand, kainate (*see* **glutamate receptor**), and for which glutamate may be the endogenous ligand. The receptor is coupled to Na^+/K^+ channels in the cell membrane, which are opened when activated by agonist.

kainic acid (2*S*,3*S*,4*S*)-2-carboxy-4-(1-methylethenyl)-3-pyrrolidineacetic acid; digenic acid; a cyclic analogue of L-glutamic acid obtained from *Digenea simplex* (a red alga). It is an amino-acid agonist for the **kainate receptor**, is a neurotoxin, and has anthelmintic properties.



kainic acid

kairomone any of a heterogeneous group of chemical messengers that are emitted by organisms of one species but benefit members of another species; they are commonly nonadaptive or maladaptive to the emitter. They include attractants, phagostimulants, and other substances that mediate the positive responses of, e.g., predators to their prey, herbivores to their food plants, and parasites to their hosts. *Compare* **allomone**, **pheromone**.

kalinin **1** *another name for* laminin 5 (*see* **laminin**). **2** a filament-associated protein of the **laminin** family. Example (precursor) human kalinin B1, also known as nicein B1 or (most commonly) laminin B1k: database code A53612, 1170 amino acids (129.27 kDa).

kallidin *an alternative name for* lysylbradykinin; *see* **bradykinin**.

kallikrein any of two groups of serine endopeptidases, EC 3.4.21.34 and EC 3.4.21.35; the active site provides a **charge-relay system**. They are widely distributed in mammalian tissues and body fluids, including blood. **Plasma kallikrein** (EC 3.4.21.34; *also called* kininogenin *or* Fletcher factor *or* serum kallikrein) cleaves Arg-|-Xaa and Lys-|-Xaa bonds, including Lys-|-Arg and Arg-|-Ser bonds in kininogen to produce bradykinin, and activates blood coagulation factors XII and VII; it is formed from prekallikrein by factor XIIa. Example (precursor): database code KAL_HUMAN, 638 amino acids (71.37 kDa). **Tissue kallikrein** EC 3.4.21.35; *other names*: glandular kallikrein; kininogenin; a serine endopeptidase that catalyses the preferential cleavage of Arg-|-Xaa bonds in small molecule substrates. Its highly selective action to release kallidin (lysyl-bradykinin) from **kininogen** involves hydrolysis of Met-|-Xaa or Leu-|-Xaa. The rat enzyme is unusual in liberating bradykinin directly from autologous kininogens by cleavage at two Arg-|-Xaa bonds. Examples: human glandular kallikrein 1 precursor (kidney/pancreas/salivary gland kallikrein): database code KLK1_HUMAN, 262 amino acids (28.86 kDa); human glandular kallikrein 2 precursor (prostate): database code KLK2_HUMAN, 261 amino acids (28.64 kDa). 3-D structures of the protein with basic proteinase inhibitor from pig have been obtained: chain a, database code NRL_2KAIA, 80 amino acids (9.10 kDa); chain b, database code NRL_2KAIB, 152 amino acids (16.48 kDa). They were formerly classed as EC 3.4.4.21 and EC 3.4.21.8, respectively.

kallistatin *or* **protease inhibitor 4** an acidic protein (in plasma) of the **serpin** family, expressed widely in human tissues. It inhibits tissue **kallikrein**, forming a 1:1 complex with it. Example (precursor) from human: database code A55560, 427 amino acids (48.50 kDa).

kanamycin an aminoglycoside antibiotic complex produced by *Streptomyces kanamyceticus*. It is made up of three components: kanamycin A (in which $R_1 = NH_2$, $R_2 = OH$; see structure), the major component, often designated as kanamycin; and two minor congeners, kanamycin B (R_1 and $R_2 = NH_2$) and kanamycin C ($R_1 = OH$, $R_2 = NH_2$). Kanamycin causes misreading during protein synthesis in bacteria, but its target

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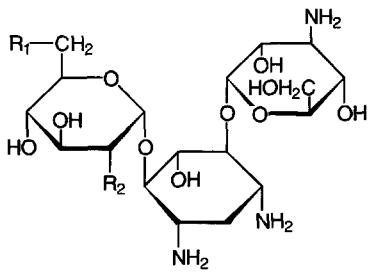
site on the ribosome is apparently different from that of streptomycin. *See also* **kanosamine**.



kanosamine 3-amino-3-deoxy-D-glucose; an amino sugar present in **kanamycin** and other antibiotics, and as free carbohydrate in fermentation broths of *Bacillus aminoglucosidicus*.

K antigen *see* **capsular antigen**.

kaolin *or* **china clay** a finely powdered hydrated aluminium silicate; it is useful as an adsorbent.

Kaposi's sarcoma a skin cancer endemic to equatorial Africa and often occurring in AIDS patients. [After Moritz Kaposi (1837–1902), Austrian dermatologist.]

kappa *symbol*: κ (lower case) *or* K (upper case); the tenth letter of the Greek alphabet. For uses *see* **Appendix A**.

kappa B *or* **κB** an element common in eukaryotic promoters. The consensus sequence is GGRNNYYCC, e.g. GGGGACTTTCC in mouse and human.

kappa chain *or* **κ chain** *symbol*: κ; one of the two types of **light chain** found in human immunoglobulins, the other type being a lambda chain. *See also* **Bence-Jones protein**.

kappa factor a protein factor that causes termination of transcription of various bacteriophage DNAs, including those of T4, T5, and T7, by *Escherichia coli* DNA-dependent RNA polymerase in a DNA site-specific manner. It is a dimer of two apparently identical 17 kDa peptide chains.

kappa particle a cell of any of several species of *Caedibacter* present in the cytoplasm of killer strains of *Paramecium aurelia*. (*Caedibacter* is a genus of Gram-negative bacterial obligate endosymbionts of this protozoan.) When kappa particles (and/or toxic constituents or products of them) are released by killer paramecia they may be lethal to sensitive paramecia (which lack both the endosymbiont and a protective genetic factor).

Karplus curve a curve describing the relation of the nuclear magnetic resonance spin–spin coupling constant and the dihedral angle. [After Martin Karplus (1930–).]

Karplus relation an equation describing the relation between the magnitude of the nuclear magnetic resonance spin–spin coupling constant, J, across three bonds and the dihedral angle, Θ, about the central bond. It is:

$$J = A + B\cos\Theta + C\cos^2\Theta,$$

where A, B, and C are coefficients that depend on the electronegativity of the substituents.

Karrer, Paul (1889–1971), Swiss organic chemist distinguished, *inter alia*, for his structural characterization of vitamin A, for the synthesis (at the same times as R. J. Kuhn) of vitamins A and B_2, and for the synthesis of vitamin E; Nobel Laureate in Chemistry (1937) 'for his investigations on carotenoids, flavins, and vitamins A and B_2' [prize shared with W. N. Haworth].

karyo+ *or* **caryo+** *comb. form* denoting the nucleus of a cell.

karyogram *an alternative name for* **idiogram**.

karyoid *an alternative name for* **nucleoid** (def. 1).

karyokinesis **1** *an alternative name for* **mitosis**. **2** division of the cell nucleus during mitosis. *Compare* **cytokinesis**.

karyon *or* **caryon** the **nucleus** of a cell.

karyophilic proteins soluble proteins that accumulate in the nucleus on microinjection into the cytoplasm of amphibian oocytes.They are not bound to chromatin or other nuclear structures. They include **nucleoplasmin** and the acidic nuclear proteins N1 to N4 of the *Xenopus* oocyte nucleus.

karyosome a compartment, located on the nucleolus of some plant species, that may support the rRNA genes as they extend from the nucleolar organizer region.

karyotype the visual appearance of the set of chromosomes of a typical somatic eukaryotic cell of a given species, individual, or cell strain. It is expressed in terms of chromosomal sizes, shapes, and number. —**karyotypic** *adj.*

kasugamine 2,4-diamino-2,3,4,6-tetradeoxy-D-*arabino*-hexose; a component of **kasugamycin** and other antibiotics.

kasugamycin an aminoglycoside antibiotic produced by a strain of *Streptomyces kasugaensis* and containing **kasugamine**. It interacts stoichiometrically with the 30S ribosomal subunit, preventing initiation of protein biosynthesis in prokaryotes; it also blocks translation in fungal systems.

kat *symbol for* katal.

katabolism *a variant spelling of* **catabolism**. —**katabolic** *adj.*

katacalcin a 21-residue peptide derived from the protein precursor of calcitonin, in which it flanks calcitonin on the C-terminal side. It is potent in lowering plasma calcium levels. It is present in normal plasma in concentrations equimolar with calcitonin, and is released rapidly by calcium infusion.

katal *symbol*: kat; a derived coherent unit for expression of enzyme activities, defined as that **catalytic activity** of an enzyme that will raise the rate of conversion of a specified chemical reaction by one mole per second in a specified assay system. There are several important points regarding usage. (1) This definition supersedes a version expressed in terms of the intensive quantity 'rate of reaction' rather than the extensive quantity 'rate of conversion', as well as earlier versions in which catalytic activity was identified with the overall rate of reaction (including the spontaneous rate) rather than with the increase in rate. (2) The katal is not an SI unit; the SI unit mol s^{-1} may be used if preferred. (3) The katal is not used to express rates of conversion themselves (for which the unit is mol s^{-1}). (4) The katal is independent of assay conditions (although the measured catalytic activity of a given system depends on assay conditions). (5) The use of **enzyme unit** (*symbol*: U) is discouraged; 1 kat $\approx 6 \times 10^7$ U; 1 U $\approx$ 16.7 nkat).

katanin a microtubule-stimulated ATPase that severs and disassembles microtubules to tubulin dimers.

Kat.f. an obsolete unit for expressing the specific activity of catalase preparations, originally defined as the rate constant for the catalysed reaction under certain conditions divided by the number of grams of enzyme in the total test volume. The rate constant is calculated from the standard equation for a unimolecular reaction using decadic logarithms and is expressed per minute. Later (apparently unintended) variations of this definition sometimes were used. [From the German *Katalasefähigkeit*, catalase capability.]

katharometer an apparatus used to determine the composition of a gas mixture by measuring its thermal conductivity.

kathode *a variant spelling* of **cathode**. —**kathodic** *adj.*

kation *a variant spelling of* **cation**.

Katz, (Sir) Bernard (1911–), German-born British biophysicist and neurophysiologist distinguished for his studies of the physiology of muscle and nerve, especially regarding the mechanism of release of acetylcholine by neural impulses; Nobel Laureate in Physiology or Medicine (1970) jointly with J. Axelrod and U. S. von Euler 'for their discoveries concerning the humoral transmittors in the nerve terminals and the mechanism for their storage, release, and inactivation'.

Kauffmann–White scheme a classification scheme for the many serotypes of the bacterial genus *Salmonella*, defined in terms of their somatic (surface) antigens and, where appropriate, their capsular and flagellar antigens.

Kautsky effect the characteristic changes with time in the flu-

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orescence emission of chlorophyll *a* that occur when dark-adapted cells or isolated chloroplasts are illuminated. The changes may be distinguished into a fast change lasting only a few seconds, and a slower change lasting a few minutes. [After Hans Kautsky (1891–1966).]

kayser a unit of **wave number** expressed as the number of wavelengths of electromagnetic radiation in 1 cm.

Kazal inhibitor an electrophoretically heterogeneous proteinaceous trypsin inhibitor and anticoagulant found in the pancreas and in pancreatic juice of a number of mammalian species. *Compare* **pancreatic trypsin inhibitor**. [After Louis Anthony Kazal (b. 1912), US physiologist.]

kb *symbol for* kilobase.

K capture *see* **electron capture**.

K cell **1** an immunocytochemically distinguishable, granule-containing cell, found in the duodenum and jejunum, that produces **glucose-dependent insulinotropic peptide**. **2** *or* **killer cell** a type of large granular mononuclear lymphocyte that can kill target cells sensitized with antibody. The K cells engage the antibody via their **Fc receptors**. They are probably identical with natural killer (NK) cells.

K chromophore any **chromophore** that gives rise to high-intensity absorption bands due to π–π conjugation. *Compare* **R chromophore**.

kDa *symbol for* kilodalton.

KDEL a tetrapeptide sequence (in the single-letter amino-acid code) at the C terminus of proteins that are to be retained in the endoplasmic reticulum (ER). An equivalent sequence is HDEL, especially in plants. The sequence is recognized by the **KDEL receptor**, and retention is thought to be mediated by continual retrieval from a post-ER compartment, as soluble ER proteins carry carbohydrate modifications assumed to have been acquired in the Golgi complex. *See also* **luminal proteins**.

KDEL receptor a transmembrane protein of the endoplasmic reticulum that recognizes and binds the tetrapeptide **KDEL**, which constitutes the C terminus of proteins destined to be retained in the endoplasmic reticulum. Such receptors are seven-transmembrane-helix proteins. An equivalent receptor in yeast for the HDEL sequence is a product of the gene *ERD2*. Example: database code ER21_HUMAN, 212 amino acids (24.54 kDa).

KDO *abbr. for* ketodeoxyoctanoate.

ke- *abbr. for keto-*.

Keilin–Hartree heart-muscle preparation a preparation of submitochondrial particles from bovine heart muscle that is capable of catalysing the reoxidation by dioxygen of NADH and succinate. [After D. Keilin (1887–1963) and E. F. Hartree (1910–94).]

Kell system a blood-group system whose antigenic determinant depends on the structure of an erythrocyte membrane glycoprotein with molecular mass 93 kDa. This glycoprotein has a long extracellular C-terminal domain with 15 cysteine residues, a short N-terminal cytoplasmic domain, and a zinc binding site of the type found in neutral endopeptidases. Example from human: database code KELL_HUMAN, 732 amino acids (82.82 kDa).

kelvin *symbol*: K; the SI base unit of thermodynamic temperature, defined as the fraction 1/273.16 of the thermodynamic temperature of the triple point of water. The symbol K is used both for thermodynamic temperature and for thermodynamic temperature interval, and supersedes °K (degree Kelvin). [After William Thomson, Lord Kelvin (1824–1907), British mathematician, physicist, and inventor, who first defined the absolute scale of temperature.]

KEM1 the symbol of a gene of yeast that encodes a nuclease specific for **G-quartets**.

Kendall, Edward Calvin (1886–1972), US physiological chemist noted for his isolation of the thyroid hormone thyroxine (1915) and especially for the isolation of a number of adrenal cortical hormones and the study (with P. S. Hench) of their actions; Nobel Laureate in Physiology or Medicine (1950) jointly with P. S. Hench and T. Reichstein 'for their discoveries relating to the hormones of the adrenal cortex, their structure and biological effects'.

Kendall's compounds a series of naturally occurring steroids of the adrenal cortex and their metabolites; they were provisionally designated by **Kendall**, using letters of the alphabet, before elucidation of their structures. They are: Kendall's compound A, 11-dehydrocorticosterone; Kendall's compound B (Reichstein's substance H), corticosterone; Kendall's compound C (Reichstein's substance C), 5α-pregnane-3α,11β,17α,21-tetrol-20-one; Kendall's compound D (Reichstein's substance A), 5α-pregnane-3β,11β,17α,20β,21-pentol; Kendall's compound E (Reichstein's substance Fa), cortisone; Kendall's compound F (Reichstein's substance M), cortisol; Kendall's compound G (Reichstein's substance D), 5α-pregnane-3β,17α,21-triol-11,20-dione; Kendall's compound H (Reichstein's substance N), 5α-pregnane-3β,21-diol-11,20-dione; Kendall's desoxy compound B (Reichstein's substance Q), cortexone, 11-deoxycorticosterone.

Kendrew, (Sir) John Cowdery (1917–97), British biophysicist and molecular biologist renowned especially for his determination by X-ray analysis of the three-dimensional structure of the myoglobin molecule; Nobel Laureate in Chemistry (1962) the prize being shared with M. F. Perutz 'for their studies of the structures of globular proteins', especially myoglobin and hemoglobin.

kephalin *a variant spelling of* **cephalin**.

kerasin *or* **cerasin** a **cerebroside** in which the fatty acyl moiety is lignoceroyl.

keratan sulfate *or (formerly)* **keratosulfate** any member of a group of glycosaminoglycans with repeat units consisting of (β1→3)-linked D-galactopyranosyl-(β1→4)-*N*-acetyl-D-glucosamine 6-sulfate and containing variable amounts of fucose, sialic acid, and mannose units. In keratan sulfate I, isolated from cornea, the carbohydrate is attached to the polypeptide backbone through *N*-acetylglucosaminyl–asparaginyl linkages, while in keratan sulfate II, isolated from cartilage and bone, the carbohydrate appears to be attached to the polypeptide backbone through *N*-acetylgalactosamine in *O*-glycosidic linkage to either serine or threonine residues. The keratan sulfates are often attached to the same polypeptide backbone as the chondroitin sulfates.

keratein the soluble product formed by reductive scission of disulfide cross-links in wool keratin on treatment with sulfhydryl compounds such as thioglycolate.

keratin any member of a class of structural fibrous scleroproteins that occur in vertebrate skin and in various specialized epidermal structures, e.g. feathers, nails, hair, hooves, horns, and quills, as well as in the cytoskeleton. They are classified into **hard keratins**, specific to hair, nails and feathers, and **cytokeratins**, which form part of the cell cytoskeleton. The hard keratins are typically sulfur-rich proteins cross-linked by disulfide bonds, having M_r in the region of 6000–20 000; the cytokeratins are larger (40 000–56 000) low-sulfur proteins. The hard keratins of mammals are largely α helical ('α keratins'), whereas those of birds and reptiles are largely β sheet ('β keratins'). However α keratin can be converted to a β-sheet conformation by reduction and heating (as in hairdressing). Example, keratin of merino wool: database code KRB2_SHEEP, 97 amino acids (10.29 kDa). Cytokeratins are intermediate-filament proteins and are of two types: I (acidic) and II (neutral to basic) (40–55 and 56–70 kDa respectively); these form microfibrillar filaments in epithelial cells. Cytokeratin is composed of complexes formed by the aggregation of at least one of each type: e.g. keratin 1 is generally associated with keratin 10. There is similarity to all other intermediate-filament proteins. Example, keratin 1 (human): database code K2C1_HUMAN, 643 amino acids (65.42 kDa); keratin 10: database code K1CJ_HUMAN, 593 amino acids (59.46 kDa).

keratinization *or* **keratinisation** **1** the process by which epidermal cells synthesize keratin. **2** the elaboration of structures

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containing keratin, especially in skin. —**keratinize** *or* **keratinise** *vb.*

keratinocyte *or* **keratocyte** any epidermal cell that produces keratin.

keratohyalin a material seen in microscopic sections in granular cells of the skin. It is thought to consist mainly of **filaggrin**.

keratosulfate *a former name for* **keratan sulfate**.

kernicterus an encephalopathy associated with degeneration and yellow pigmentation of basal ganglia and other nerve cells in the spinal cord and brain, caused by the severe unconjugated bilirubinemia occurring in newborn infants and occasionally in older children with hereditary unconjugated hyperbilirubinemia.

kerosene *or* **kerosine** *an alternative name (esp. US) for* **paraffin** (def. 2).

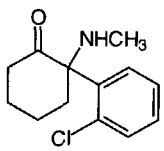
Kerr effect *an alternative name for* **electric birefringence**. [After John Kerr (1824–1907), Scottish physician.]

kestose **1** *or (sometimes)* **6-kestose** *O*-β-D-fructofuranosyl-(2→6)-*O*-β-D-fructofuranosyl-(2→1)-α-D-glucopyranose; a trisaccharide widely distributed in plants, especially in the bulbs and tubers of monocotyledons, and formed artificially when yeast invertase is incubated with a 50% solution of sucrose. The name is derived from the fact that it was discovered at the Tate and Lyle research laboratories, then at Keston, Kent, UK. **2 1-kestose** isokestose; inulobiosyl glucose; *O*-β-D-fructofuranosyl-(2→1)-*O*-β-D-fructofuranosyl-(2→1)-α-D-glucopyranose; an isomer and congener of 6-kestose. *See also* **neokestose**.

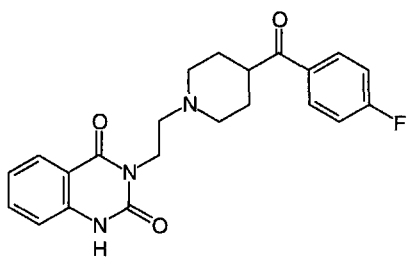
ket+ *a variant form of* **keto+** (sometimes before a vowel).

ketal *see* **acetal**.

ketamine (±)-2-(2-chlorophenyl)-2-(methylamino)cyclohexanone; a dissociative anesthetic with cataleptic and analgesic effects, possibly through acting as an *N*-methyl-D-aspartate (excitatory amino acid) receptor antagonist.



ketanserin 3-[2-[4-(4-fluorobenzoyl)-1-piperidinyl]ethyl]-2,4[1*H*,3*H*]-quinazolinedione; an antagonist to α_1 **adrenoceptors**, H_1 **histamine receptors**, and 5-HT_2 **5-hydroxytryptamine receptors**. A clinically effective hypotensive agent, it differentiates between 5-HT_1 and 5-HT_2 receptors with high specificity; within adrenoceptors and histamine receptors it is less specific.



ketene **1** ethenone; CH_2=C=O. **2** any substituted **ketene** (def. 1).

ketimine any **imine** that is an analogue of a ketone; the general structure is R_2C=NR′ where R is any organyl group and R′ may be any organyl group or H. *Compare* **aldimine**.

keto **1** carbonyl group, =CO, in any ketone. **2** describing a class of chemical compounds of the general formula R–CO–R′ (where R, R′ are not H). The term is often used to distinguish such compounds from isomeric compounds of another class, e.g. keto sugar. **3** a nonpreferred term, often still used, to denote the presence of a substituent in an organic compound of a double-bonded oxygen atom that is part of a ketonic structure. The recommended term is **oxo**.

keto+ **1** *or (sometimes before a vowel)* **ket+** *comb. form* indicating ketonic or derived from a ketone; e.g. ketal, ketoaldose, ketol. **2** *or (sometimes before a vowel)* **keton+** *comb. form* denoting of or pertaining to a **ketone body** or bodies; e.g. ketoacidosis, ketogenesis, ketonuria. **3** *prefix (in chemical nomenclature)* denoting a ketonic derivative of an indicated organic compound; **oxo** now recommended.

keto- *abbr.*: *ke-*; an optional prefix to the (semi)systematic name of a monosaccharide or monosaccharide derivative containing an uncyclized ketonic carbonyl group, used to stress its acyclic nature. *Compare* ***aldehydo-***, **keto**, **keto+**.

keto acid any organic (carboxylic) acid containing a **keto** (def. 3) group; the recommended term is an oxo acid.

ketoacidosis a type of **acidosis** caused by enhanced production of **ketone bodies** by the ketogenic pathway. Excessive production of ketone bodies has harmful effects not only in lowering the blood pH but in promoting the excretion of K^+ and Na^+ by the kidney, leading to cation depletion. It occurs in conditions where **ketogenesis** occurs faster than the **ketone bodies** produced can be metabolized; this results most often from hormonal imbalance, especially insulin deficiency, when fatty acids are mobilized at an excessive rate from adipose tissue and transported to the liver, where they are converted to ketone bodies. In humans, a plasma level of up to 8 mmol L^{-1} is considered safe and may be beneficial, but in disease states levels may reach up to 20 mmol L^{-1}, contributing to life-threatening situations. —**ketoacidotic** *adj.*

ketoaldonic acid any monosaccharide formally derived from an aldonic acid by oxidation of a secondary alcoholic hydroxyl group to an oxo group.

ketoaldose any monosaccharide containing both an aldehydic and a ketonic carbonyl group.

ketoconazole a complex derivative of imidazole, clinically useful as an antimycotic. It impairs ergosterol synthesis in fungal cell membranes, thereby increasing their permeability.

ketodeoxyoctanoate *abbr.*: KDO; 2-keto-3-deoxy-D-octanoate; 3-deoxy-D-*manno*-2-octulosonate; an acid present in lipopolysaccharides of the outer membranes of certain Gram-negative bacteria.

keto–enol tautomerism a type of **tautomerism** in which the keto and enol forms of a compound are in equilibrium, the change corresponding to the migration of a hydron and a shift of bonding electrons. *Compare* **amino–imino tautomerism**.

ketofuranose any **ketose** in the **furanose** form.

ketogenesis the metabolic production of **ketone bodies**. The pathway starts with the formation of acetoacetyl-CoA (I) from two molecules of acetyl-CoA by **acetyl-CoA *C*-acetyltransferase** (EC 2.3.1.9); I then reacts with a further molecule of acetyl-CoA, in a reaction catalysed by mitochondrial **hydroxymethylglutaryl-CoA synthase**, to form (*S*)-3-hydroxy-3-methylglutaryl-CoA (II); II is then cleaved to acetoacetate and acetyl-CoA by **hydroxymethylglutaryl-CoA lyase**. The reactions of ketogenesis occur in higher animals, localized entirely in mitochondria; the liver is the main site of synthesis, but kidney, and possibly also small intestine, and adipose tissue may play a part in some situations.

ketogenic forming, or having the quality of being convertible into ketone bodies by metabolic processes.

α-ketoglutarate *a nonpreferred (though often used) name for* 2-oxoglutarate; 2-oxo-1,5-pentanedioate; a compound that has important roles in carbohydrate and amino-acid metabolism, especially in transamination reactions and as a component of the **tricarboxylic-acid cycle**.

α-ketoglutaric dehydrogenase *see* **oxoglutarate dehydrogenase (lipoamide)**.

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2-keto-L-gulonate *or (preferably)* **2-oxo-L-gulonate** L-*xylo*-2-hexulosonate; a compound obtained from sorbitol and an important intermediate in the manufacture of **ascorbic acid**.

ketoheptose any **ketose** having a chain of seven carbon atoms in the molecule. Eight enantiomeric pairs of such compounds are possible.

ketohexokinase EC 2.7.1.3; *systematic name*: ATP:D-fructose 1-phosphotransferase; *other name*: hepatic fructokinase. An enzyme that catalyses the phosphorylation by ATP of D-fructose to D-fructose-1-phosphate with release of ADP. The enzyme occurs in liver (in the soluble fraction), in muscle, intestine, and renal cortex, and in bacteria. It also phosphorylates some other ketoses (e.g. 5-dehydro-D-fructose, D-sorbose, D-tagatose). This enzyme is often referred to as fructokinase, although this is the recommended name for the enzyme EC 2.7.1.4, which forms D-fructose 6-phosphate (*see* **fructokinase**). In mammals, some fructose can be phosphorylated to fructose 6-phosphate by **hexokinase**. Example from rat: database code KHK_RAT, 298 amino acids (32.71 kDa).

ketohexose any **ketose** having a chain of six atoms in the molecule. Four enantiomeric pairs of such compounds are possible, these being the D and L isomers of fructose, psicose, sorbose, and tagatose.

α-ketoisocaproate *or (preferably)* **α-oxoisocaproate** 4-methyl-2-oxopentanoate; an intermediate in the biosynthesis of L-leucine. *See* **leucine and valine biosynthesis**.

α-ketoisovalerate *or (preferably)* **α-oxoisovalerate** 3-methyl-2-oxobutanoate; an intermediate in the biosynthesis of L-leucine, L-valine, and pantothenic acid. *See* **leucine and valine biosynthesis**.

ketol **1** any organic compound that is both a ketone and an alcohol, especially an α-ketol (i.e. acyloin), one in which the two functions are adjacent. **2** the strongly reducing group, $HO–CH_2–CO–$, that is characteristic of an α-ketol. It is present, e.g., in ketoses and certain corticosteroids.

ketol-acid reductoisomerase EC 1.1.1.86; *systematic name*: *(R)*-2,3-dihydroxy-3-methylbutanoate:$NADP^+$ oxidoreductase (isomerizing); *other names*: dihydroxyisovalerate dehydrogenase (isomerizing); acetohydroxy-acid isomeroreductase. An enzyme, found in chloroplasts, that catalyses the reversible reaction:

(R)-2,3-dihydroxy-3-methylbutanoate + $NADP^+$ = *(S)*-2-hydroxy-2-methyl-3-oxobutanoate + NADPH.

It is a component of the pathways for isoleucine and valine biosynthesis. Example from *Spinacia oleracea* (spinach); tetramer of similar but nonidentical chains: database code ILV5_SPIOL, 595 amino acids (63.68 kDa).

ketol condensation the enzyme-catalysed formation of certain **ketols** (def. 1) by addition of an acyl moiety of one α-oxo acid to another α-oxo acid to form an α-hydroxy-β-oxo acid. It occurs, e.g., in the condensations catalysed by acetolactate synthase (EC 4.1.3.18); these involve either two molecules of pyruvate condensing to form α-acetolactate and CO_2, or one molecule of pyruvate and one of α-oxobutyrate condensing to form α-aceto-α-hydroxybutyrate and CO_2. The main products are biosynthetic precursors of valine and leucine, and of isoleucine, respectively.

ketolysis *a term sometimes used to* describe the oxidation, for energy production, of ketone bodies by extrahepatic tissues.

α-keto-β-methylvalerate *or (preferably)* **α-oxo-β-methylvalerate** 3-methyl-2-oxopentanoate; the biosynthetic precursor of, and catabolic product of, L-isoleucine.

keton+ *a variant form of* **keto+** (def. 2) (sometimes before a vowel).

ketone **1** any compound containing a carbonyl group, >C=O, joined to two carbon atoms. **2** *the functional class name for* any **ketone** (def. 1) that does not have a trivial name, e.g. ethyl methyl ketone.

ketone body any of the three substances: (1) acetoacetate, formed enzymically from acetyl-CoA; (2) D-3-hydroxybutyrate (β-hydroxybutyrate), formed by liver mitochondrial 3-hydroxybutyrate dehydrogenase (EC 1.1.1.30) from acetoacetate; or (3) acetone, formed by spontaneous decarboxylation of acetoacetate. Ketone bodies may accumulate in excessive amounts in the body in starvation, diabetes mellitus, or in other defects of carbohydrate metabolism. They are formed in the post-absorptive state and during more prolonged fasting, and can be used as an energy source as an alternative to glucose, sparing glucose and thus indirectly muscle protein, since the carbon source for glucose synthesis under such conditions derives from muscle amino acids. Biosynthesis involves the formation of **hydroxymethylglutaryl-CoA**, which is cleaved to acetoacetate and acetyl-CoA by **hydroxymethylglutaryl-CoA lyase**; it occurs largely in the liver, but to a small extent also in kidney. Utilization of ketone bodies in peripheral tissues involves conversion by **3-oxo-acid CoA-transferase** of acetoacetate to acetoacetyl-CoA, which is then converted to two molecules of acetyl-CoA by **acetyl-CoA *C*-acetyltransferase**. Although not a ketone, 3-hydroxybutyrate is classed as a ketone body because it exists in an equilibrium with acetoacetate that depends on the redox state in the liver mitochondria. To determine the extent of ketone body formation, it is therefore necessary to include 3-hydroxybutyrate in the analysis.

ketonemia *or (esp. Brit.)* **ketonaemia** an abnormally high concentration of **ketone bodies** in the blood.

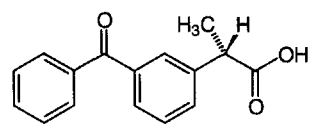
ketonic of, relating to, or having the properties of a **ketone** or a **keto** (def. 1) group.

ketonize *or* **ketonise** to convert into or become converted into a ketone. —**ketonization** *or* **ketonisation** *n.*

ketonuria a condition in which there is an abnormally large excretion of ketone bodies in the urine.

ketopentose any **ketose** having a chain of five carbon atoms in the molecule. Two enantiomeric pairs of such compounds are possible, these being the D and L isomers of ribulose and xylulose.

ketoprofen 2-(3-benzoylphenyl)propionic acid; a nonsteroidal anti-inflammatory agent; it is one of the substituted propionic acids that inhibit prostaglandin-endoperoxide synthase (EC 1.14.99.1). *See also* **ibuprofen**.



(*S*)-ketoprofen

ketopyranose any **ketose** in the **pyranose** form.

ketose any monosaccharide in the acyclic form of which the actual or potential carbonyl group is nonterminal, i.e. ketonic. The systematic names and many of the trivial names of ketoses have the ending '+ulose'. The position of the (potential) carbonyl group is indicated by a prefixed locant (e.g. 3-ketose, 5-nonulose), which may be omitted from the name of a 2-ketose when no ambiguity can arise. The term is frequently modified by an infix indicating the number of carbon atoms in a chain in the molecule; thus **ketopentose**, **ketotetrose**, etc. *Compare* **aldose**.

ketosis any clinical condition in which there are abnormally high concentrations of **ketone bodies** in the tissues. The condition is usually accompanied by acidosis. *See also* **ketogenesis**. —**ketotic** *adj.*

ketosteroid *a former name for* **oxosteroid**.

keto sugar *a common name for* any **ketose**.

ketotetrose either of two **ketoses** having a chain of four carbon atoms in the molecule, these being the enantiomeric pair D- and L-*glycero*-tetrulose.

β-ketothiolase *see* **acetyl-CoA *C*-acyltransferase**.

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ketotriose the single achiral **ketose** having a chain of three carbon atoms in the molecule and known as dihydroxyacetone, or glycerone.

kex2 a structural gene for pre-pro-alpha mating type polypeptide in *Saccharomyces cerevisiae*. It gives rise to the designation Kex2 site, a cleavage site (Arg-|-Arg or Lys-|-Arg) for **kexin** in the processing of the mating polypeptide and several extracellular fungal proteins.

kexin EC 3.4.21.61; *other names*: yeast Kex2 protease; proteinase YSCF; prohormone-processing endoprotease; paired-basic endopeptidase. An enzyme that catalyses the cleavage of Lys-Arg-|-Xaa and Arg-Arg-|-Xaa bonds to process yeast α-factor pheromone and killer toxin precursors. Example, kexin precursor from yeast: database code KEX2_YEAST, 814 amino acids (89.90kDa); the human enzyme with the same specificity (and EC number) is neuroendocrine convertase 1 precursor, database code NEC1_HUMAN, 753 amino acids (84.03 kDa). *See also* **furin**, ***kex2***, **proopiomelanocortin**.

kg *symbol for* kilogram.

KHF *abbr. for* killer cell helper factor (i.e. **interleukin 2**).

Khorana, Har Gobind (1922–), Indian organic chemist and biochemist renowned, *inter alia*, for his chemical synthesis of coenzyme A, various codon-containing polyribonucleotides, and a double-stranded DNA segment containing the gene for the tyrosine tRNA of *Escherichia coli* and its (larger) precursor RNA; Nobel Laureate in Physiology or Medicine (1968) jointly with R. W. Holley and M. W. Nirenberg 'for their interpretation of the genetic code and its function in protein synthesis'.

kicksorter a multichannel pulse-height analyser, especially one used to distinguish between radioisotopes by sorting them according to the energies (i.e. 'kicks') of their emitted radiations.

kidney either of a pair of organs of vertebrates concerned with osmoregulation and the elimination of nitrogenous waste products. Kidneys of different species vary in structure according to the animal's mode of life, but their basic design and function is the same. Each kidney is enclosed in a capsule and is made up of an outer cortex and an inner medulla, and contains numerous **nephrons** and their associated blood supply. The nephrons filter constituents from the blood to form urine, which is discharged from the kidney via the ureter.

kieselguhr *an alternative name for* **diatomaceous earth**.

killed vaccine any suspension of killed (or otherwise inactivated) microorganisms or virus used as an antigen to produce immunity.

killer cell any cell that is cytotoxic to *in vitro* cell cultures, e.g. killer T-lymphocytes and macrophages. Antibody-dependent cell-mediated cytotoxicity may be displayed by a number of cell types, e.g. by human monocytes or interferon-activated neutrophils, which can kill antibody-coated tumour cells, and by **NK cells**, which kill hybridoma cells through the NK cell FcγRII receptor. *See also* **K cell**.

killer-cell helper factor *abbr.*: KHF; *an alternative name for* **interleukin 2**.

killer factor an RNA molecule responsible for the lethal property of **killer strains** of yeast.

killer strain any strain of cells that is able to kill sensitive cells of the same species, e.g. some strains of yeast and *Paramecium*. *See also* **kappa particle**, **killer factor**.

killer T-lymphocyte any T lymphocyte that is able to kill target cells. Killer T-lymphocytes are produced in response to viral infection or an allogeneic tissue graft, and are specifically cytotoxic to host cells infected with virus or to grafted cells carrying the major histocompatibility antigens of the donor, respectively.

kilo- *symbol*: k; an SI prefix denoting 10^3 times.

kilobase *symbol*: kb; a unit of length of a polynucleotide equal either to 1000 base residues in a single-stranded polynucleotide or to 1000 base pairs in a double-stranded polynucleotide.

kilocalorie *or* **kilogram calorie** *or (esp. in nutrition)* **Calorie** a non-SI unit of heat or energy equal to 10^3 cal_{IT}. *See* **calorie**.

kilodalton *symbol*: kDa; a unit of molecular mass equal to 10^3 **daltons**.

kilogram *symbol*: kg; the SI base unit of mass, and also the fundamental unit of mass in the metric system; it is equal to the mass of the international prototype of the kilogram.

kilogram calorie *an alternative name for* **kilocalorie**.

kinase any phosphotransferase enzyme that transfers a phosphate group, usually from ATP. Kinases are divided into EC sub-subclasses according to the nature of the phosphate-accepting group: EC 2.7.1 – phosphotransferases with an alcohol group as acceptor; EC 2.7.2 – phosphotransferases with a carboxyl group as acceptor; EC 2.7.3 – phosphotransferases with a nitrogenous group as acceptor; EC 2.7.4 – phosphotransferases with a phosphate group as acceptor. The name is also used for enzymes that transfer a phosphate group from other nucleoside triphosphates. *Compare* **dikinase**, **pyrophosphokinase**, **thiokinase**.

+kinase *suffix (in the trivial name of an enzyme)* **1** designating a **kinase** or, by extension in certain instances, one that transfers some other inorganic oxo-acid group, e.g. **sulfokinase**. **2** designating an enzyme that activates a zymogen by proteolysis, e.g. **enterokinase**, **streptokinase**, **thrombokinase**.

kinasing *a jargon term for* the act or process of labelling the 5′ end of a nucleic-acid molecule or fragment with phosphorus-32 by reaction with adenosine 5′-[α-^{32}P]triphosphate and the enzyme T4 polynucleotide kinase. This is a step in the **chemical cleavage method** for sequencing DNA and RNA.

kinematic viscosity *symbol*: ν; the dynamic viscosity, η, of a fluid divided by its density, ρ, i.e. $\nu = \eta/\rho$.

kinesin microtubular motor protein, composed of two heavy chains and several light chains, that uses the energy of ATP hydrolysis (ATPase activity in the head of the heavy chain) to move along microtubules, mostly to the plus end but in some cases to the minus end (e.g. in *Drosophila*). Kinesins are involved in organelle transport, and in mitosis and meiosis. Example, kinesin heavy chain from human: database code KINH_HUMAN, 963 amino acids (109.56 kDa). *See also* **dynein**.

kinetensin *or* **neurotensin-related peptide** (*abbr.*: NRP) the nonapeptide Ile-Ala-Arg-Arg-His-Pro-Tyr-Phe-Leu; it has **neurotensin**-like immunoreactivity and is isolated from human, bovine, and canine plasma.

kinetic **1** of or relating to the motions of material bodies and the forces and energies associated therewith; of or relating to motion. **2** of or relating to the rate(s) of change of physical or chemical systems. **3** of or relating to **kinetics**.

kinetic energy *symbol*: E_k *or* T *or* K; the energy possessed by a material body by virtue of its motion, determined by the work necessary to bring it to rest.

kinetic proofreading a suggested mechanism of twice using the same Michaelis kinetic ability of an enzyme system to distinguish between two substrates C and D. The essential features of the mechanism are contained in the following reaction scheme, shown for substrate C, but identical in form if substrate C is replaced by D.

$$\mathrm{C + E} \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} \mathrm{EC} \dashrightarrow \mathrm{EC^*} \xrightarrow{k_3} \mathrm{E + product}$$
$$k_4 \uparrow\downarrow k_{-4}$$
$$\mathrm{E + C^*} \xrightarrow[k_5]{} \mathrm{C}$$

The second step is enzymically coupled to an energy source, typically the hydrolysis of a nucleoside triphosphate, and is strongly enough driven to be essentially irreversible. EC*, a high-energy intermediate, may *either* react to give free enzyme plus product *or* diffuse into the solution where it decomposes

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to free enzyme plus the nonproduct C*, which can further decompose to C. According to kinetic proofreading, the incorrect intermediate, ED*, diffuses into the solution and decomposes faster than it reacts to give the wrong product, i.e. for ED* $k_3 << k_{-4}$, while for EC* $k_3 > k_{-4}$. In this way, the better binding of C is used twice, once in the formation of EC and again in the binding of the intermediate EC*. If the discrimination in the formation of the initial complex is f, a second factor of f may theoretically be attained, giving a total discrimination of f^2.

kinetics 1 the branch of chemistry concerned with studying rates of chemical reactions. 2 the branch of mechanics concerned with the effects of forces on the motions of material bodies.

kinetin 6-furfurylaminopurine; N^6-furfuryladenine; an artefactual compound formed by autoclaving DNA. It exhibits **cytokinin** activity in plants and was originally thought to be a naturally occurring substance. *Compare* **Kinetin**.

Kinetin *a proprietary name for* **hyaluronidase**. *Compare* **kinetin**.

kinetochore a specialized assembly of proteins that bind to the **centromere** and also attach to **microtubules** growing out from **centrosomes** during mitosis. They are involved in the separation of chromosomes into the daughter cells. They are composed of **centromere-binding proteins**.

kinetochore microtubule *see* **mitotic spindle, prometaphase**.

kinetoplast a DNA-rich organelle located within an expanded region of a mitochondrion lying close to the **basal body** in members of the order **Kinetoplastida**. The kinetoplast is self-replicating and divides before the nucleus in cell division.

Kinetoplastida an order of protozoans whose members are characterized by the presence of a **kinetoplast** in the mitochondrion. It includes the genera *Trypanosoma*, *Leishmania*, and *Crithidia*.

kinetosome *an alternative name for* **basal body**.

King–Altman method a general method for obtaining steady-state expressions for enzymic mechanisms with n enzyme-containing intermediates $EX_1 \ldots EX_n$. First, a simple geometrical pattern describing the mechanism is drawn. Second, all possible patterns, consisting of $(n-1)$ lines, that interconnect the possible enzyme forms are drawn; closed loops are forbidden. In general there will be $m!/(n-1)!(m-n+1)!$ patterns, where m is the number of interconversion steps. Third, n expressions for $(d[EX_i]/dt[E_{tot}]) = 0$ in terms of the rate constants are set out and solved by determinant methods, using the fact that

$$\sum_{i=1}^{n} ([EX_i]/[E_{tot}]) = 1$$

where $[E_{tot}]$ is the total enzyme concentration. [After E. L. King and C. Altman, who described it in 1956.]

kinin 1 *or* **kinin-hormone** any member of a varied group of linear polypeptides that constitute a class of so-called tissue or local hormones. Each is locally released from diffuse stores in the body, not having specialized glands of secretion, and is rapidly inactivated at the site of release. Among the most important are **angiotensins**, **bradykinin**, **substance P**, colostrokinin, urinary kinins, and **secretin**. 2 **kinin-9** *an alternative name (sometimes) for* **bradykinin**. 3 **kinin-10** *an alternative name (sometimes) for* kallidin (lysylbradykinin). *See* **bradykinin**. 4 *an alternative name for* **cytokinin**.

kininase any enzyme concerned in the natural breakdown of a **kinin** (def. 1). Included are kininase I (*or* lysine carboxypeptidase, EC 3.4.17.3), a carboxypeptidase circulating in plasma that inactivates bradykinin and possibly also kallidin, and kininase II (peptidyl-dipeptidase A, EC 3.4.15.1), *also known as* **angiotensin-converting enzyme**.

kininogen any inactive precursor of a **kinin** (def. 1).

kininogenin *an alternative name for* **kallikrein**.

kinked-helix model of duplex DNA a speculative model of the structure of double-stranded DNA in chromatin, proposed in 1975 by F. **Crick** and A. **Klug** to account for the high degree of folding of the DNA (to about one seventh of its length). In this model, based on the B form of duplex DNA, all the base pairs of the double helix remain intact but a sharp turn, or kink, of 95–100° occurs every 20 base pairs along the duplex. At this point one base pair has become unstacked from an adjacent pair through change of the conformation of the deoxyfuranose ring of a nucleotide residue from one of its possible staggered conformations to another. It was suggested that a kink might render several base pairs more easily available for specific interaction with a protein, and that a similar type of folding might occur in double-stranded DNA in other situations, especially when closely associated with protein.

kinomere *an alternative term for* **centromere**.

Kirkwood–Riseman theory of hydrodynamic properties of complex structures a theory providing an approximate method for computing the friction of a structure made up of identical subunits. A linear or coiled polymer is approximated as a string of beads, each with identical hydrodynamic properties, while an oligomeric protein is modelled as a cluster of identical subunits each with identical hydrodynamic properties.

Kirkwood theory of dielectric polarization of polar liquids an extension of the Onsager theory in which the dielectric constant of the central molecule and its first shell of neighbours is considered to differ from its macroscopic value. [After John Gamble Kirkwood (1907–59).]

Kirkwood theory of ion–dipole interactions a model in which the electrical contribution to the chemical potential of an ion having an arbitrary charge distribution is calculated with the aid of the Debye–Hückel theory and in which the Born relation between the free energy of solvation of a spherical ion and the dielectric constant of the solvent is generalized to include ions of arbitrary charge distribution.

Kirkwood–Westheimer theory of electrostatic effects on acid dissociation constants an extension and amplification of the Bjerrum theory of the influence of substituents on acid dissociation constants, the molecules and ions entering into ionization equilibria being treated as cavities of low dielectric constant. [After John Gamble Kirkwood (1907–59) and Frank Henry Westheimer (1912–), US biochemist.]

kirromycin *or* **mocimycin** an antibacterial antibiotic isolated from *Streptomyces collinus* and others. It specifically interacts with **elongation factor** EF-Tu (*see* **EF-T**) and prevents the release of EF-Tu from the bacterial ribosome after GTP hydrolysis. In the absence of ribosomes, the antibiotic induces an EF-Tu-dependent hydrolysis of GTP.

kistrin a protein isolated from the venom of the Malayan pit viper, *Agkistrodon rhodostoma*. It contains the **RGD** sequence and binds to a platelet adhesion site. It is a potent platelet aggregation inhibitor and antagonist of a family of glycoproteins that mediate aggregation. *For example, see* **disintegrin**.

KIT a family of genes encoding plasma membrane class III receptor tyrosine kinases. The viral gene, v-*kit*, is the oncogene of the Hardy–Zuckerman 4 strain of acutely transforming feline sarcoma virus. The product of the protooncogene c-*kit* has five immunoglobulin-like loops in the extracellular domain; the cytoplasmic region contains a tyrosine kinase domain with an insert region, and is myristoylated. Interaction with its ligand, steel factor (*see* **stem cell factor**), brings about dimerization, leading to enhanced autophosphorylation and binding of phosphatidylinositol 3-kinase and phospholipase Cγ. Kit and its ligand are highly expressed in small-cell lung cancer and a significant proportion of testicular germ cell tumours. Example from human (precursor): database code KKIT_HUMAN, 976 amino acids (109.74 kDa).

Kjeldahl, Johan Gustav Christoffer Thorsager (1849–1900), Danish brewing chemist; first director of the Carlsberg Laboratory, Copenhagen.

Kjeldahl flask a small pear-shaped glass flask with a long neck, as used in the **Kjeldahl method**.

Kjeldahl method a method for the determination of the total nitrogen in an organic compound or mixture of compounds.

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The sample, in a **Kjeldahl flask**, is digested in hot, concentrated sulfuric acid in the presence of a catalyst, usually one containing mercury, copper, or selenium; the nitrogen in the sample is thereby converted to ammonium hydrogen sulfate. The ammonium formed may be estimated by neutralization and steam distillation of the resultant ammonia into a known amount of acid, the residual acid being determined by titration, or it may be estimated by **nesslerization** or with an ammonium electrode.

Kleinschmidt technique a technique for preparing monolayers of DNA for electron microscopy in which the DNA molecules are bound to a film of denatured basic protein, e.g. cytochrome *c*, on the surface of an aqueous solution. The DNA molecules are consequently brought from a three-dimensional conformation to a two-dimensional one by adsorption to the protein layer. The DNA–protein complex is then transferred to a solid surface, e.g. an electron microscope grid or collodion film, dried, and contrasted with heavy metals by shadowing or staining. The tendency of **ssDNA** to fold back on itself with the formation of intramolecular base pairs can be overcome by using formamide (which denatures short base-paired regions) or by replacing cytochrome *c* with DNA-unwinding proteins, which have high affinity for ssDNA. The method may also be applied to RNA. [After Albrecht K. Kleinschmidt (1916–), German microbiologist.]

Klenow enzyme *or* **Klenow fragment** *a name sometimes used for* the larger (75 kDa) of the two fragments formed by the treatment of *Escherichia coli* DNA polymerase I with subtilisin in the presence of DNA. The Klenow enzyme retains the polymerase activity and the single-strand-specific 3′→5′ exonuclease activities but lacks the 5′→3′ exonuclease activity of DNA polymerase I. It is useful in sequencing single-stranded DNA. [After Hans Klenow (1923–), Danish biochemist.]

Klotz plot *a name sometimes given to* a plot of the reciprocal form of an equation describing ligand binding at multiple independent sites on, e.g., a macromolecule. It has the form:

$$1/\bar{\nu} = (1/nk)(1/[A]) + 1/n,$$

where $\bar{\nu}$ is the average number of ligand molecules bound per molecule of the macromolecule, n is the number of binding sites per macromolecule, [A] is the molar concentration of free ligand molecules, and k is the intrinsic association constant. If the equation correctly describes the equilibria involved, a plot of $1/\bar{\nu}$ versus $1/[A]$ gives a straight line of slope $(1/nk)$ and with an intercept on the $1/\bar{\nu}$ axis of $1/n$ and on the $1/[A]$ axis of $-1/k$. [After Irving Myron Klotz (b. 1916), US biochemist.]

Klug, (Sir) Aaron (1926–), Lithuanian-born South African and subsequently British molecular biologist distinguished for his determination of the structure of transfer RNA and for his contributions to the understanding of the three-dimesional structure of complexes of proteins and nucleic acids, especially tobacco mosaic virus and the nucleosome, through his invention of the technique of image reconstruction; Nobel Laureate in Chemistry (1982) 'for his development of crystallographic electron microscopy and his structural elucidation of biologically important nucleic acid–protein complexes'.

KMEF group *abbr. for* keratin-myosin-epidermin-fibrinogen group; a group of proteins that have in common an α-type X-ray diffraction pattern. Some of these may show a β-type pattern in some conditions. Silk fibroin, which normally occurs with a β structure, is often included in the KMEF group.

knallgas bacteria *or* **hydrogen bacteria** any of a number of bacterial species that can obtain energy from the **knallgas reaction** i.e. the oxidation of dihydrogen to water by dioxygen. They include some *Alcaligenes* and *Pseudomonas* spp. and *Paracoccus denitrificans*. [From the German, *Knallgas*, an explosive mixture of hydrogen and oxygen.]

knallgas reaction the energy-yielding direct oxidation of dihydrogen by dioxygen occurring in certain bacteria (*see* **knallgas bacteria**). The reaction is:

$$2\,H_2 + O_2 \rightarrow 2\,H_2O + \text{energy}.$$

knockout indicating an animal in which function of a gene has been deleted by genetic engineering techniques.

Knoop's hypothesis the hypothesis that fatty acids are metabolically oxidized by the successive removal of two-carbon fragments as acetic acid. *See also* **beta oxidation**. [After Franz Knoop (1875–1946), German physiologist and biochemist.]

Knop solution an aqueous solution containing the major inorganic constituents required for the growth of cells of higher plants, namely calcium nitrate, potassium nitrate, magnesium sulfate, potassium dihydrogen phosphate, and potassium chloride. [After J. A. L. W. Knop (1817–1901), German chemist.]

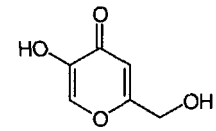
Knox plot *(in high-performance liquid chromatography)* a plot of relative separation efficiency versus flow rate, useful in determining the optimal conditions for a desired separation. [After John H. Knox.]

Koch phenomenon a cell-mediated hypersensitivity reaction in which inflammation of guinea-pig skin, when injected with living or dead *Mycobacterium tuberculosis*, is very much greater in animals actively infected with the organism than in uninfected animals injected with dead organisms. [After (Heinrich Hermann) Robert Koch (1843–1910), German bacteriologist, who isolated the bacillus in 1882.]

Köhler, Georges Jean Franz (1946–95), German immunologist famous for his discovery (with C. Milstein) of the technique of using cell fusion to generate a clonal cell population capable of producing unlimited quantities of a pure antibody; Nobel Laureate in Physiology or Medicine (1984) jointly with N. K. Jerne and C. Milstein 'for theories concerning the specificity in development and control of the immune system and the discovery of the principle for production of monoclonal antibodies'.

kojibiose the disaccharide 2-*O*-α-D-glucopyranosyl-D-glucopyranose.

kojic acid 5-hydroxy-2-(hydroxymethyl)-4*H*-pyran-4-one; a metabolite from *Aspergillus oryzae* and *A. terreus*. It can be obtained in large amounts and has some industrial application.



Kok effect the sharp difference in yield of photosynthesis above and below the compensation point. Below compensation, where respiration can supply intermediates at a greater rate than the rate of photosynthesis, the yield is about twice as great as above compensation, where CO_2 has presumably to be drawn into the process. [After Bessel Kok (1918–81) Dutch-born US plant physiologist.]

Kornberg 1 Arthur Kornberg (1918–), US biochemist distinguished especially for his discovery and purification of the enzyme DNA polymerase and its use to synthesize segments of DNA molecules and viral DNA; Nobel Laureate (1959) in Physiology or Medicine jointly with S. Ochoa 'for their discovery of the mechanisms in the biological synthesis of ribonucleic acid and deoxiribonucleic [*sic*] acid'. **2 Hans Leo Kornberg** (1928–) German-born British biochemist notable for his studies of intermediary metabolism in bacteria.

Kornberg enzyme *an alternative name for* DNA polymerase I. *See* **DNA polymerase**. [After A. **Kornberg**.]

Korsakoff's psychosis *see* **Wernicke–Korsakoff syndrome**.

Koshland model *see* **induced-fit theory**.

Kossel, Karl Martin Leonhard Albrecht (1853–1927), German physiological chemist distinguished for his researches on nucleins (i.e. nucleoproteins), for his discovery of adenine, cytosine, thymine, and uracil as breakdown products of nucleic

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acids, for his discoveries of histone and histidine, and for his studies of the composition of proteins and its relation to their biological functions; Nobel Laureate in Physiology or Medicine (1910) 'in recognition of the contributions to our knowledge of cell chemistry made through his work on proteins, including the nucleic substances'.

Kr *symbol for* krypton.

Krabbe's disease *an alternative name for* **galactosylceramide lipidosis**. [After Knudd Haraldsen Krabbe (1885–1961), Danish physician.]

KRB *abbr. for* Krebs Ringer bicarbonate; *see* **Krebs mammalian Ringer**.

Krebs **1 (Sir) Hans Adolf Krebs** (1900–81), German-born British biochemist renowned for his work on intermediary metabolism and in particular for the discovery of the two cyclic metabolic pathways named after him (*see* **Krebs cycle** def. 1,2) Nobel Laureate in Physiology or Medicine (1953) 'for his discovery of the citric acid cycle' [prize shared with F. A. Lipmann]. **2 Edwin Gerhard Krebs** (1918–), US biochemist; Nobel Laureate in Physiology or Medicine (1992) jointly with Edmond H. Fischer 'for their discoveries concerning reversible protein phosphorylation as a biological regulatory mechanism'.

Krebs–Cohen dismutation The anaerobic reaction summarized as:

$$2\text{-oxoglutarate} + NH_4^+ \rightarrow \text{succinate} + \text{glutamate} + CO_2 + H^+.$$

It has been shown to occur in pigeon heart and breast muscle, rat and guinea-pig renal cortex, and rat-liver mitochondria. It is the sum of two reactions:

$$2\text{-oxoglutarate} + H_2O + NAD^+ \rightarrow \text{succinate} + CO_2 + NADH + H^+,$$

and

$$2\text{-oxoglutarate} + NADH + NH_4^+ \rightarrow \text{glutamate} + NAD^+ + H_2O.$$

[After H. A. **Krebs** and Philip Pacy Cohen (1908–93), US biochemist.]

Krebs cycle *an alternative name (sometimes) for* **1 tricarboxylic-acid cycle. 2 ornithine–urea cycle**.

Krebs–Henseleit cycle *an alternative name (sometimes) for* the **ornithine–urea cycle**. [After H. A. **Krebs** and Kurt Henseleit (1908–73).]

Krebs–Henseleit Ringer bicarbonate *see* **Krebs mammalian Ringer**.

Krebs–Kornberg cycle *an alternative name (sometimes) for* **glyoxylate cycle**. [After H. A. **Krebs** and H. L. **Kornberg**.]

Krebs mammalian Ringer any of several media devised for the suspension of mammalian tissues. Their composition was essentially based on the available analytical data for the inorganic constituents of blood plasma of a number of mammalian species. In the first version (1932), **Krebs–Henseleit Ringer bicarbonate**, the buffer was bicarbonate-CO_2, while in the second (1933), **Krebs original Ringer phosphate**, it was phosphate. In improved versions (1950), often referred to respectively as **Krebs Ringer bicarbonate** (*abbr.*: KRB) and (calcium-free) **Krebs Ringer phosphate** (*abbr.*: KRP), a mixture of organic acids and glucose was substituted for part of the NaCl in the first two versions, to resemble as closely as possible the state of the tissues in the intact animal. Also, an additional medium, low in phosphate, bicarbonate, and CO_2, was devised. *See also* **Ringer's solution**.

Krebs' manometer fluid a solution containing 44 g NaBr, 0.3 g Triton X-100, and 0.3 g Evans' Blue in 1000 mL of water; D = 1.033. The standard pressure (760 mmHg) in mm of manometer fluid is 10 000. Other detergents may be substituted for the Triton X-100 in equivalent proportions.

K region a region in a carcinogenic polycyclic aromatic hydrocarbon molecule in which there is a carbon–carbon bond having ordinary double-bond rather than aromatic character and that takes part in addition reactions; e.g. the bond between atoms C-9 and C-10 in phenanthrene. It has been suggested that carcinogenicity in such molecules is determined by the existence in them of an active K region. *Compare* **L region**.

kringle a conserved protein domain of about 85 amino acids that is held in a characteristic three-dimensional conformation by three internal disulfide bridges. It is so-named because its two-dimensional representation resembles that of the kringle, a Scandinavian pastry of characteristic shape. It was first described in prothrombin, but homologous domains, with the characteristic shape and similarly positioned disulfides, are found in plasminogen and (both tissue-type and urokinase-type) plasminogen activators. *See also* **Appendix E**.

Kronig–Kramers transform any of a set of mathematical relations describing the response of a system to a perturbation such as light. These relations allow the calculation of optical rotary dispersion from circular dichroism (ellipticity) and vice versa, and describe the relationship between dispersion and absorption. [After R. de L. Kronig and Hendrik Anthony Kramers (1894–1952), Dutch physicist, who independently devised them in 1926 and 1927, respectively.]

KRP *abbr. for* Krebs Ringer phosphate; *see* **Krebs mammalian Ringer**.

Krüppel a protein involved in the segmentation of the embryo and in the differentiation of the malpighian tubules in insects (e.g. *Drosophila*). It is a nuclear, chromatin-associated protein, encoded by a **gap gene**, and is a member of a subfamily of C_2H_2-type zinc-finger proteins. Mutant *krüppel* larvae lack eight body segments. Example from *Drosophila melanogaster*: database code KRUP_DROME, 466 amino acids (50.74 kDa). [From German *Krüppel*, cripple.]

KS/hst a human oncogene, with no known viral counterpart, whose product is related to **fibroblast growth factor** and is expressed in **Kaposi's sarcoma**. Database code: HBG4_HUMAN, 206 amino acids (22.02 kDa).

k(T) *symbol for* rate constant (alternative to k, used when distinction of a rate constant from the Boltzmann constant is necessary).

Kuhn, Richard Johann (1900–67), Austrian-born German chemist and biochemist notable, *inter alia*, for his reintroduction (with H. Lederer) of the technique of adsorption chromatography by demonstrating the resolution of carotene into three isomers, for his synthesis (at the same times as P. Karrer) of vitamins A and B_2, for his isolation of nicotinamide from heart muscle and of riboflavin from milk, and for the synthesis of the coenzyme flavin mononucleotide, riboflavin 5′-phosphate; Nobel Laureate in Chemistry (1938) 'for his work on carotenoids and vitamins'.

Kunitz and Northrop inhibitor *see* **pancreatic trypsin inhibitor**.

Kunitz inhibitor the best known of the three distinguishable **soybean trypsin inhibitors**. The term has been extended to refer to any type of protease inhibitor that contains consensus sequences known as **Kunitz domains** (*see* **Appendix E**). These include some serine protease inhibitors. Such domains have also been identified in some α-amyloid precursor protein isoforms.

Kunitz (tryptic) unit a measure of tryptic activity based on the extent to which trypsin-containing samples can digest casein under standard conditions often used to determine the relative amounts of Kunitz and Bowman–Birk type trypsin inhibitors present in samples, comparison being made between tryptic activity and chymotryptic activity. Crystalline trypsin has an activity of 6 Kunitz units per mg.

Kupffer cell a type of nonmotile, mononuclear phagocytic cell. Such cells line the sinusoids of the liver. [After Karl Wilhelm von Kupffer (1829–1903), German anatomist.]

kuru a transmissible **spongiform encephalopathy** of humans, characterized by degeneration of the nervous system and found among the Fore people of Papua New Guinea. It is a **prion** disease, transmitted through funerary practices thought to have involved endocannnibalism. The brains of victims of this and **Gerstmann–Sträussler syndrome** contain so-called kuru plaques which have been shown to stain positively with antibodies

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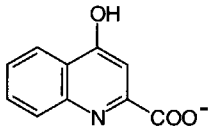
against prion protein in patients with Gerstmann–Sträussler syndrome. It has become extremely rare since cannibalism ceased in the late 1950s.

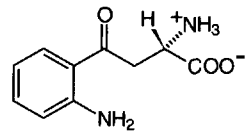
kwashiorkor a form of severe malnutrition of children occurring in tropical or near-tropical regions. It is generally believed to be caused by a dietary deficiency of protein, but not of other energy-producing foodstuffs. The condition commonly develops when, after prolonged breast feeding, the child is weaned onto a diet inadequate in protein. *Compare* **marasmus**.

kynurenate 4-hydroxyquinaldate; 4-hydroxy-2-quinoline carboxylate; the anion of kynurenic acid and an intermediate in the conversion of **kynurenine** to quinaldate.



kynureninase EC 3.7.1.3; *systematic name*: L-kynurenine hydrolase; a pyridoxal-phosphate-containing enzyme that hydrolyses L-kynurenine to anthranilate and L-alanine. It also acts on 3′-hydroxykynurenine and some other (3-arylcarbonyl)-alanines.

kynurenine 3-anthraniloylalanine; L-kynurenine is a metabolite on the degradative pathway of tryptophan, is found in the urine especially in pyridoxal (vitamin B_6) deficiency, and is an intermediate in the synthesis of nicotinic acid from tryptophan.



kyotorphin the analgesic dipeptide, L-Tyr-L-Arg, isolated from bovine brain; D-kyotorphin is L-Tyr-D-Arg.

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LI

l *symbol for* 1 litre (alternative to **L**). **2** liquid.

l *symbol for* length (alternative to *L*).

l- *prefix (in chemical nomenclature)* denoting levorotatory; now obsolete, use (–)-; *see* **optical isomerism**.

L *symbol for* **1** litre (alternative to l). **2** a residue of the α-amino acid L-leucine (alternative to Leu). **3** an atom of hydrogen that may be one of *either* protium *or* deuterium. **4** linking number. **5** light chain (def. 1) (of an immunoglobulin).

L *symbol for* **1** Avogadro constant (alternative to N_A). **2** latent heat. **3** radiance.

L- a configurational prefix used in designating the absolute configuration of chiral compounds of certain classes; *see* **D/L convention**.

La *symbol for* lanthanum.

label **1** *or (sometimes informally)* **tag** any (radioactive or stable) isotope substituted in a proportion of the molecules of a particular compound so that the translocation and/or the chemical or biochemical transformation of the compound may be followed. *See also* **tracer**. **2** *or (sometimes)* **marker** an easily recognizable chemical group (which can be radioactive) attached to a molecule or incorporated within a structure. **3** to attach or apply such a label. The following particular uses of the terms label or labelled have individual entries (*see also* the list at **labelling**): **affinity label**, **electron-dense label**, **immunoassay**, **mixed labelled**, **multiply labelled**, **nonselectively labelled**, **photoaffinity label**, **radioactive label**, **selectively labelled**, **singly labelled**, **specifically labelled**, **spin label**, **uniformly labelled**.

labelled compound *or (US, usually)* **labeled compound** a compound bearing a **label** (def. 1, 2). An isotopically labelled compound is a compound in which one or more atoms of a proportion of the molecules have been replaced by a (radioactive or stable) isotope; i.e. it is a mixture of an isotopically unmodified compound with one or more analogous isotopically substituted compound(s). In some cases, the amount of isotopically unmodified compound may be small. This is particularly the case for ^2H compounds, when near 100% replacement is possible. *See also* **carrier-free**.

labelling *or (US, usually)* **labeling** **1** the attribute of being labelled. **2** the act or process of chemically introducing a **label** (def. 1, 2) into a compound either by substitution or by synthesis, or of incorporating such a label into a material or structure. The following particular uses of the term labelling have individual entries (*see also* the list at **label**): **conjugation labelling**, **double labelling**, **enzyme labelling**, **ferritin labelling**, **fluorescein labelling**, **generally labelled**, **hapten-sandwich labelling**, **iodine labelling**.

labile **1** describing a chemical compound that is prone to spontaneous change or decomposition; relatively unstable. **2** describing an atomic or molecular grouping in a chemical compound that unusually readily dissociates from the compound; loosely attached. **3** describing a chemical bond that very easily ruptures or is ruptured. —**lability** *n.*

labile factor *an alternative name for* factor V; *see* **blood coagulation**.

labile phosphate the amount or proportion of any phosphate that is readily liberated from a phosphate-containing compound by hydrolysis in 1 M HCl at 100 °C within 7–10 min (*hence also sometimes known as* **seven-minute phosphate** *or* **ten-minute phosphate**). These conditions were selected originally for estimating the two terminal phosphate groups of ATP. The following compounds are included in the group (percentage hydrolysis in parentheses): phosphocreatine (100), ATP (67), ADP (50), aldose 1-phosphate (100), pyrophosphate (100).

labilize *or* **labilise** to render **labile** (*esp.* def. 3). —**labilization** *or* **labilisation**, **labilizer** *or* **labiliser** *n.*

lac any of various resinous substances secreted by certain plants or insects, used in the manufacture of lacquers.

lac *symbol for* the genetic system of *Escherichia coli* that controls the organism's ability (lac^+) or inability (lac^-) to metabolize **lactose**. *See also* ***lac* operon**, ***lac* repressor**.

laccase any of a group of copper–protein enzymes (EC 1.10.3.2) of low specificity, that catalyse the oxidation of both *o*- and *p*-quinols by dioxygen to form the corresponding semiquinones and two molecules of water. They are so-called because such an enzyme was first found in the lac (or lacquer) tree (*Rhus verniciflua*); however, they are now known to be widely distributed in plants and fungi.

lacI the structural gene for ***lac* repressor**, the repressor of the *lac* operon.

***lac* operon** *or* **lactose operon** a genetic system, or **operon**, of *Escherichia coli* that controls the synthesis of the inducible enzyme β-D-galactosidase (*see* **galactosidase**). It is probably the most intensively studied group of *E. coli* genes. It consists of a linear sequence (5′ end to 3′ end of the coding strand) of two control sites, designated *p* and *o*, followed by three structural genes, designated *z*, *y*, and *a*; *p* is the promoter (concerned with RNA-polymerase binding), *o* is the operator (binding site for repressor), *z* is the gene for β-galactosidase, *y* is the gene for the **permease**, and *a* is the gene for thiogalactoside transacetylase (an enzyme of uncertain physiological function). Immediately preceding the *p* site is a regulatory gene designated *i* (concerned with synthesis of ***lac* repressor**).

***lac* repressor** a protein encoded by the *lacI* gene, that controls the expression of structural genes coding for enzymes involved in lactose metabolism in the *Escherichia coli* genome; in the absence of inducer it binds with high affinity to the operator site of the ***lac* operon**. It is a homotetramer and specifically recognizes a 23 base-pair DNA sequence in the *lac* operator by means of its four N-terminal domains (headpieces), each of 51 amino-acid residues; each subunit also has one allosteric binding site for an inducer. The repressor is a typical **helix-turn-helix** protein and gives its name to a subfamily. Database code: LACI_ECOLI, 360 amino acids (38.55 kDa).

lact+ *a variant form of* **lacto+** *(before a vowel)*.

lactalbumin *or* **α-lactalbumin** a Ca^{2+}-binding protein of the **lactalbumin/lysozyme family**, present in the milk of virtually all mammals. In the case of non-ruminants it is the predominant protein in whey. It contains 123 amino-acid residues, 40 of which are identical with and occupy corresponding positions to those of lysozyme. It is a noncatalytic regulatory protein whose presence is required for **lactose synthase** to transfer a galactose residue from UDPgalactose to D-glucose; hence it is also known as B protein of lactose synthase. It causes the substrate for *N*-acetyllactosamine synthase to change from *N*-acetylglucosamine to glucose to give lactose and UDP. Protein B had, therefore, been called a **'specifier' protein** The genes for lysozyme and α-lactalbumin arose evolutionarily from a common ancestral gene. Example (precursor) from human: database code LCA_HUMAN, 142 amino acids (16.21 kDa); five motifs.

lactalbumin/lysozyme family a protein family whose members are characterized by six conserved motifs. Common members are α-lactalbumin (*see* **lactalbumin** (def. 2)) and **lysozyme**; 3-D structures are known.

lactam any intramolecular cyclic amide produced by the formal removal of a molecule of water between the amino and the carboxyl groups of an amino acid other than an α-amino acid. A prefix (as in β-lactam) may be used to designate the position of the amino group in the parent compound. A lactam commonly exists in tautomeric equilibrium with its corresponding **lactim**.

***β*-lactam antibiotic** any member of a class of natural or semi-synthetic antibiotics whose characteristic feature is a strained,

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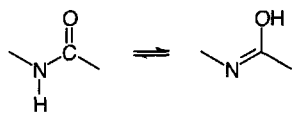
four-membered β-lactam ring (*see* **lactam**). They include the **penicillins** and many of the **cephalosporins**.

β-lactamase any member of a group of constitutive or inducible enzymes (EC 3.5.2.6); *systematic name*: β-lactam-hydrolase. They are produced by certain strains of various bacterial species and can catalyse the hydrolysis of the **lactam** linkage in one or more β-lactam antibiotics, leaving a substituted β-amino acid; they thereby inactivate the antibiotic. The enzymes are of varying specificity, some acting more rapidly on penicillins (**penicillinases**), some more rapidly on cephalosporins (**cephalosporinases**); the latter were formerly classified separately as EC 3.5.2.8.The β-lactamases can be inhibited by various substances, such as **clavulanic acid**. There are several classes: class A (or type I) enzymes have seven motifs; class B (or type II) enzymes have a zinc cofactor. Class A example, Men-1 broad spectrum (hydrolyses penicillins and many cephalosporins) from *Escherichia coli*: database code BLM1_ECOLI, 263 amino acids (28.18 kDa). Class B example (hydrolyses carbapenems and penicillins) from *Bacteroides fragilis*: database code BLAB_BACFR, 249 amino acids (27.23 kDa).

lactam–lactim tautomerism a form of **tautomerism** occurring in lactam–lactim interconversion as a result of migration of a hydron between the nitrogen atom and the oxygen atom. It represents a special case of amide–imidol tautomerism.



lactase *a trivial name for* any **β-D-galactosidase**. Some hydrolyse certain other glycosides, including α-L-arabinosides, β-D-fucosides, and β-D-glucosides.

lactase deficiency a condition of humans in which there is a congenital or acquired deficiency of lactase (i.e. **β-galactosidase**) in the mucosa of the small intestine leading to failure to digest lactose and to **lactose intolerance**. The condition is rare in infants and young children but is more common in healthy adolescents and adults; its frequency varies considerably in different population groups: it is more prevalent in native populations of Australia and Oceania, east and south-east Asia, tropical Africa, and the Americas (45–95%) than in those of central and northern European ancestry (<25%).

lactate **1** α-hydroxypropionate; 2-hydroxypropanoate; the anion, CH_3–CH(OH)–COO^-, derived from **lactic acid**. It occurs naturally as D(–)-lactate (i.e. (*R*)-2-hydroxypropanoate) and L(+)-lactate (i.e. (*S*)-2-hydroxypropanoate). L(+)-lactate is formed by anaerobic glycolysis in animal tissues, and DL-lactate is found in sour milk, molasses, and certain fruit juices. Bacterial **lactic-acid fermentations** produce either the D(–) or L(+) enantiomer or the racemate (DL) depending on the individual organism. **2** any salt or carboxylic ester of lactic acid. **3** to secrete milk; *see* **lactation**.

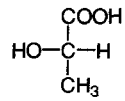
lactate dehydrogenase any of several enzymes that interconvert **lactate** and pyruvate. **L-Lactate dehydrogenase** (EC 1.1.1.27; *abbr.*: LD *or* LDH) acts on L-lactate and NAD^+. Example from human (heart muscle form): database code LDHH_HUMAN, 333 amino acids (36.47 kDa); this is a homotetramer, but some are heterotetramers of the heart muscle (H) and skeletal muscle (M) forms (the five isoenzymes are: LD_1, H_4; LD_2, H_3M; LD_3, H_2M_2; LD_4, HM_3; and LD_5, M_4). In clinical chemistry the assay of LD_1 (*known also as* α-hydroxybutyrate dehydrogenase *or* HBD) can be of use in diagnosing myocardial infarction, in which it reaches a peak at 2–3 days after the infarct, and in hemolytic crisis of sickle-cell anemia, since this isoenzyme is the predominant form in cardiac muscle and red cells. **D-Lactate dehydrogenase** (EC 1.1.1.28) acts on D-lactate and NAD^+. **L-Lactate dehydrogenase (cytochrome)** (EC 1.1.2.3) acts on L-lactate and ferricytochrome *c* and is a flavohemoprotein (FMN is coenzyme). **D-Lactate dehydrogenase (cytochrome)** (EC 1.1.2.4) acts on D-lactate and ferricytochrome *c* and is a flavoprotein (FAD is coenzyme). **D-Lactate dehydrogenase (cytochrome *c*-553)** (EC 1.1.2.5) acts on D-lactate and ferricytochrome *c*-553 and is present in *Desulfovibrio vulgaris*. These enzymes are very widely distributed, catalysing the interconversion of pyruvate and lactate.

lactation **1** the secretion of milk by the mammary gland. **2** a complete period of milk secretion from about the time of parturition to that of weaning. *See also* **lactate** (def. 3).

lacteal **1** of, relating to, or resembling milk; milky. **2** (of lymph vessels) containing or conveying **chyle**. **3** any blind-ended lymph vessel that carries chyle from a villus of the small intestine to the thoracic duct.

lactic pertaining to, or derived from, milk.

lactic acid α-hydroxypropionic acid; 2-hydroxypropanoic acid; a reasonably strong acid (pK_a = 3.86 at 25 °C). In biological systems it normally exists largely as its anion, **lactate** (def. 1). It is also useful as a preservative of foodstuffs.



lactic-acid bacterium any bacterium in which lactate is the main metabolic product. Lactic-acid bacteria belong chiefly to the genera *Lactobacillus* and *Streptococcus*, and some are of commercial importance, e.g. in the manufacture of fermented foods.

lactic-acid cycle *an alternative name for* **Cori cycle**.

lactic-acid fermentation *a general name for* **heterolactic fermentation** and/or **homolactic fermentation**.

lactic acidosis a clinical condition characterized by a persistent raised blood lactate concentration, usually above 5 mmol L^{-1}, with a lowered blood pH. The condition may be caused by severe exercise, cardiovascular insufficiency, hypoxia, shock, drug intoxication, and some inborn errors of metabolism. *Compare* **hyperlactatemia**.

lactide any intermolecular cyclic ester formed by self-esterification from two (or more) molecules of a hydroxy carboxylic acid. *Compare* **lactone**.

lactifer a special cell, found in the bark of the rubber tree (*Hevea*), in which rubber latex accumulates.

lactim any intramolecular cyclic carboximidic acid produced by the formal removal of a molecule of water between the amino and the carboxyl groups of an amino carboxylic acid other than an α-amino acid. A prefix (as in β-lactim) may be used to designate the position of the amino group in the parent compound. A lactim commonly exists in tautomeric equilibrium with its corresponding **lactam**.

lactitol 4-*O*-β-D-galactopyranosyl-D-glucitol; a disaccharide used as a sweetener.

lacto+ *or (before a vowel)* **lact+** *comb. form* indicating milk.

lactobacillic acid (1*R-cis*)-2-hexylcyclopropanedecanoic acid; 11,12-methyleneoctadecanoic acid; a lipid constituent of various microorganisms, including *Lactobacillus arabinosus*.

Lactobacillus a genus of Gram-positive, anaerobic or facultatively aerobic, straight or curved bacilli or coccobacilli. Their metabolism is fermentative and all species form lactate as the major end product of glucose fermentation. Various species of lactobacilli are important in the preparation of certain fermented foods, e.g. cheese, yoghurt, sauerkraut.

***Lactobacillus bulgaricus* factor** *an alternative name for* **pantetheine**.

***Lactobacillus casei* factor** *an alternative name for* **folic acid**.

lactobionic acid the **aldonic acid** obtained by the oxidation of lactose.

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lactochrome *a former name for* **riboflavin**.

lactoferrin *or* **lactotransferrin** an iron(III)-binding protein present in milk. Its level in human plasma may be elevated in pancreatitis.

lactoflavin *or* **lactoflavine** *a former name for* **riboflavin**.

lactogen **1** any agent that stimulates the secretion of milk. **2** **placental lactogen** *an alternative name for* **choriomammotropin**. —**lactogenic** *adj.*

lactogenic hormone *an alternative name for* **prolactin**.

β-lactoglobulin *see* **beta lactoglobulin**.

lactonase **1** EC 3.1.1.17; *recommended name*: gluconolactonase; *systematic name*: D-glucono-1,5-lactone lactonohydrolase; *other name*: aldonolactonase. An enzyme that catalyses the reaction:

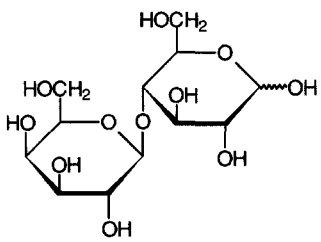
D-glucono-1,5-lactone + H_2O = D-gluconate;

it also acts on a wide range of hexono-1,4-lactones. Example from *Zymomonas mobilis*: database code GNL_ZYMMO, 320 amino acids (34.73 kDa); homodimer. **2** **1,4-lactonase** *or* **γ-lactonase** EC 3.1.1.25; an enzyme that specifically hydrolyses 1,4-lactones having 4–8 carbon atoms to the corresponding 4-hydroxyacids.

lactone any intramolecular cyclic ester produced by the formal removal of a molecule of water between the hydroxyl and the carboxyl groups of a molecule of a hydroxy carboxylic acid other than an α-hydroxy acid. A prefix (as in β-lactone) may be used to designate the position of the hydroxyl group in the parent compound. *Compare* **lactide**.

lactoperoxidase *a special name for* **peroxidase** (def. 2) from milk. It also catalyses the oxidation of iodide to iodine, hence it is useful in radioiodine labelling of proteins and other biological materials under mild conditions.

lactose *or (formerly)* **milk sugar** *the trivial name for* the **disaccharide** 4-*O*-β-D-galactopyranosyl-D-glucose. It constitutes roughly 5% of the milk of almost all mammals (human milk 6.7%; cow's milk 4.5%). It occurs rarely in plants, e.g. in the anthers of *Forsythia* spp. *See also* **allolactose**.



lactose fermenter *jargon term for* any genus, species, or strain of microorganism that ferments lactose.

lactose intolerance a syndrome occurring in humans in response to the ingestion of lactose (in milk) due to a congenital or acquired **lactase deficiency** in the mucosa of the small intestine. The failure to hydrolyse lactose leads to accumulation of the disaccharide within the intestine and consequent osmotically induced net fluid secretion into the gut, rapid intestinal transit, and acid stools due to bacterial fermentation of lactose. The condition is particularly prevalent in the Orient.

lactose operon *see* ***lac***.

lactose permease an H^+–lactose symporter in *Escherichia coli*. It has 12 transmembrane helices but is not very closely related to most other members of the superfamily. Database code LACY_ECOLI, 417 amino acids (46.45 kDa).

lactose synthase EC 2.4.1.22; *systematic name* UDPgalactose:D-glucose 4-β-D-galactotransferase; *other name*: UDP-galactose–glucose galactosyltransferase. An enzyme that catalyses the reaction:

UDPgalactose + D-glucose = UDP + lactose.

In mammary gland the protein comprises *N*-acetyllactosamine synthase, the A protein, and α-lactalbumin (*see* **lactalbumin**), the B protein, both of which are required for lactose synthesis.

lactose-tolerance test a procedure used in the investigation of suspected **lactase deficiency**. Blood-glucose concentrations are estimated before an oral dose of lactose (1 g per kg body mass) and thereafter at 30-min intervals for 2 h. In normal individuals an increase of at least 30 mg per 100 ml (0.167 mM) in the blood-glucose concentration above the fasting value is observed.

lactosuria the presence of lactose in the urine. It is not uncommon during late pregnancy and lactation, or if the flow of milk is prevented.

lactosyl either of the glycosyl groups formed from lactose by detaching the anomeric (α or β) hydroxyl group on C-1.

lactotransferrin *an alternative name for* **lactoferrin**.

lactotroph any of a class of irregular, granulated, acidophilic cells of the anterior pituitary gland that secrete prolactin. Their number increases greatly during pregnancy.

lactotrophic describing any agent that induces normal growth and development of the mammary gland and sustains it.

lactotropic describing any agent that acts on the mammary gland to induce changes in its metabolism.

lactotropic hormone *an alternative name for* **prolactin**.

lactotropin *an alternative name for* **prolactin**.

lactoyl the acyl group, CH_3–CH(OH)–CO–, derived from lactic acid.

lactulose *the trivial name for* 4-*O*-β-D-galactopyranosyl-D-fructofuranose; a semisynthetic disaccharide, prepared from lactose, that is sweeter than lactose but less sweet than sucrose. Concentrated solutions of lactulose are useful clinically as an osmotic laxative by virtue of the inability of enzymes of the small intestine to hydrolyse lactulose to absorbable monosaccharides. On ingestion it therefore passes unchanged into the colon, where it acts partly directly to increase the water content of the bowel by osmosis and partly indirectly through breakdown by commensal saccharolytic bacteria to simple organic acids, with resultant lowering of colonic pH and further osmotic uptake of water.

lactyl *a former term for* **lactoyl**.

lacY a gene in *Escherichia coli* for **lactose permease**.

L1 adhesion molecule a type I membrane glycoprotein involved in neuron–neuron adhesion, neurite fasciculation, outgrowth of neurites, etc. It is a member of the immunoglobulin superfamily, and has fibronectin domains. Example (precursor) from human: database code CAML_HUMAN, 1257 amino acids (139.77 kDa).

Laetrile *see* **amygdalin**.

laevo- *a variant spelling (esp. Brit.) of* **levo-**.

laevo+ *a variant spelling (esp. Brit.) of* **levo+**.

laevodopa *a variant spelling (esp. Brit.) of* **levodopa**.

laevorotation *a variant spelling (esp. Brit.) of* **levorotation**.

laevulose *a variant spelling (esp. Brit.) of* **levulose**.

LAF *abbr. for* lymphocyte-activating factor (i.e. **interleukin 1**).

lagging strand the DNA strand that is synthesized by the joining together of short **Okazaki fragments**, giving the effect of continuous 3′ to 5′ synthesis in the direction of fork movement during the discontinuous replication of duplex DNA. *Compare* **leading strand**.

lag phase **1** the initial phase of the growth of a bacterial culture during which the rate of increase of cell numbers remains static, before rising to a value determined by environmental conditions. The extent of the lag phase is determined by the cultural history of the cells of the inoculum and the chemical and physical conditions of the medium into which they are placed. **2** a period of comparatively low activity after the start of an enzymic reaction that involves enzymes that act at a surface, e.g. phospholipases. It is due to the slow formation of the complex between the enzyme and the substrate interface. Once this has been formed the reaction accelerates.

lake to lyse erythrocytes, especially by suspending them in a hypotonic medium.

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Laki–Lorand factor *abbr.*: LLF *or* L-L factor; *an alternative name for* factor XIII; *see* **blood coagulation**.

lambda *symbol*: λ (lower case) *or* Λ (upper case); the eleventh letter of the Greek alphabet. For uses *see* **Appendix A**.

lambda chain *or* **λ chain** *symbol*: λ; one of the two types of **light chain** of human immunoglobulins, the other type being a kappa chain. Example, V region (4A) from human: database code LV0A_HUMAN, 117 amino acids (12.37 kDa).

lambda phage *or* **λ phage** a **temperate phage** that infects *Escherichia coli* and contains linear duplex DNA, which circularizes during infection; the genome is 48 514 bp. Important gene clusters include those for the head and tail genes, recombination (*att*, *int*, *xis*, *α*, *β*, *γ*), lysis, and regulatory genes. Of the regulatory genes (*c*III, *N*, *c*I, *cro*, *c*II, *O*, *P*, *Q*), two are immediate-early genes, *cro* and *N*; *cro* prevents synthesis of the repressor (*see* **prophage**) and turns off expression of immediate-early genes, including itself, after its product, cro, binds to *O*. Lambda phage is an example of the antitermination mechanism of phage control (*see* **antiterminator**); *N* codes for an antitermination factor that allows transcription to proceed through the terminator to the delayed-early genes, *c*II and *c*III, and *Q*, codes for an antitermination factor that allows host RNA polymerase to proceed to the late (lytic) genes. The lytic cycle is repressed by expression of *c*I, the product of which acts at the operator *O* to prevent use of the promoter *P*. Lambda phage has been widely used as a vector in cDNA technology; foreign DNA can be inserted into the chromosome, and some foreign genes can be expressed using the lambda promoters. The linear DNA has cohesive ends that, when the DNA circularizes, associate to form the ***cos* site** (cohesive end site), which is important in packaging. The *cos* site has been exploited in the formation of **cosmids**.

lambda pipette *colloquial term for* a pipette used for the transfer of volumes in the microlitre range.

lambda repressor *or* **λ repressor** the product of gene *c*I; it is responsible for maintenance of phage λ **prophage**. Its product binds to the operator associated with the RNA polymerase promoter, thus preventing RNA polymerase from initiating transcription. The phage genome then cannot enter the lytic cycle. Mutants in this gene cannot maintain **lysogeny**. Example from bacteriophage λ: database code RPC1_LAMBD, 236 amino acids (26.05 kDa); and from related phage 434: database code S32822, 210 amino acids (22.96 kDa). 3-D structures, including complexes with **operators**, are known.

Lambert–Beer law *another name for* **Beer–Lambert law**.

Lambert's law (of absorption) a physical law in which **Bouger's law** was re-expressed; put into modern terms, it states that the fraction of monochromatic light (or other electromagnetic radiation) absorbed by a system is independent of the incident **radiant power**, Φ_0. The law holds only if Φ_0 is small and other factors such as reflection, scattering, and photochemical reactions are negligible. *See also* **Beer–Lambert law**. [After Johann Heinrich Lambert (1728–77), German mathematician and physicist who stated it in 1760.]

lamella (*pl.* **lamellae**) any thin layer, membrane, or platelike structure, e.g. one of the series of double membranes that carry the photosynthetic pigments in chloroplasts, one of the thin layers of calcified bone matrix, or one of the spore-bearing gills of the fruiting bodies of mushrooms or related fungi. —**lamellar** *or* **lamellate** *adj.*

lamellar phase one type of **liquid-crystalline phase**.

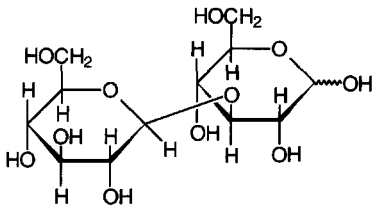
lamin any of a group of intermediate-filament proteins that form the fibrous matrix (**nuclear lamina**) on the inner surface of the nuclear envelope. They are classified as lamins A, B, and C. Examples, all from *Mus musculus*; lamin A: database code LAMA_MOUSE, 665 amino acids (74.21 kDa); lamin B_1: database code LAM1_MOUSE, 584 amino acids (66.75 kDa); lamin C: database code LAMC_MOUSE, 574 amino acids (65.45 kDa). *See also* **gliadin**.

lamina (*pl.* **laminae**) **1** any thin plate or layer, e.g. of bone or mineral. **2** *(in botany)* **a** the blade of a leaf or petal. **b** the flattened part of the thallus of certain algae. *See also* **basal lamina**, **nuclear lamina**. —**laminar** *adj.*

laminar flow a form of nonturbulent flow of a fluid in which parallel layers (laminae) of the fluid are moving in the same direction but with different velocities.

laminar-flow cabinet *another name for* **safety cabinet**.

laminaribiose the disaccharide, 3-*O*-*β*-D-glucopyranosyl-D-glucose; a unit of the seaweed polysaccharide **laminarin**.



pyranose form

laminarin a *β*-1,3-glucan that functions as a reserve polysaccharide in some brown algae (*Laminaria* spp.). It contains **laminaribiose**.

laminin a glycoprotein that is the major constituent of basement membranes. It consists of three chains, bound to each other by disulfide bonds into a cross-shaped molecule having the appearance of one long and three short arms with globules at each end (the three chains are wound together in a helical conformation for two thirds of their length, but diverge at the N-terminal end into the three arms that form the apex and side arms of a cross). The molecule interacts with procollagen type IV. Laminin mediates the attachment, migration, and organization of cells into tissues during embryonic development by interacting with other extracellular-matrix components. The precursor sequences of the three chains (all human) are: A, database code LMA_HUMAN, 3075 amino acids (336.78 kDa); B1, database code LMB1_HUMAN, 1786 amino acids (197.84 kDa); B2, database code LMB2_HUMAN, 1609 amino acids (177.41 kDa). Laminins of varying composition and sequence have been categorized as laminins 1 to 5. Laminin 5 is also known as **kalinin**.

laminin receptor any of a number of proteins, especially **integrins** (*see also* **VLA**) that bind laminin, interacting with it to promote cell adhesion and migration.

Lamm equation a general hydrodynamic equation describing the mass transport of a two-component system during ultracentrifugation. It is:

$$dc_2/dt = (1/x)\, d\{x[D(dc_2/dx) - c_2 s\omega^2 x]\}/dx,$$

where c_2 is the concentration of solute molecules at distance x from the axis of rotation, D is the translational diffusion constant, ω is the angular velocity, and s is the sedimentation coefficient.

lampbrush chromosome any of the large diplotene chromosomes found in the oocytes of many animals. They are up to 1 mm long and are covered with loops projecting in pairs from most chromomeres; each loop has a core of DNA and is the site of active gene expression.

lamprin a self-aggregating extracellular cartilage protein of lampreys, aggregates of which form fibres rich in beta structure. It is a major structural protein isolated from the annular cartilage of the lamprey, similar in amino-acid composition to **elastin**, but it does not contain desmosine or isodesmosine. Examples (precursors) from *Petromyzon marinus*: lamprin 1.9-12/10: database code LAMP_PETMA, 139 amino acids (13.24 kDa); lamprin 1.8-10: database code LAMA_PETMA, 119 amino acids (11.32 kDa); these two are seemingly formed by alternative splicing from the same gene.

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Lan *symbol for* lanthionine.

lan+ *comb. form* indicating wool. [From Latin *lana*, wool.]

Landsteiner, Karl (1868–1943), Austrian-born US pathologist and immunologist distinguished for his discoveries of the human blood groups. He designated A, B, and O (in 1901), factors M and N (in 1927), and factor Rh (in 1940); Nobel Laureate in Physiology or Medicine (1930) 'for his discovery of human blood groups'.

Landsteiner–Weiner antigen *abbr.*: LW antigen; *see* **Rhesus factor**.

lane any of a set of parallel tracks resulting from the simultaneous separation of similar samples by one-dimensional zone electrophoresis or chromatography in thin-layer media.

Langendorff perfused heart a nonworking rodent heart preparation maintained *in vitro* by perfusion into the aorta with an oxygenated fluid so that the fluid circulates primarily into the coronary arteries. It is useful for studying the metabolism of heart muscle. A number of improvements of the original preparation have been made since its introduction. [After O. Langendorff (1853–1909), German physiologist.]

Langerhans, Paul (1847–88), German physician and anatomist who first described the **islets of Langerhans**.

Lang–Levy pipette a type of constriction micropipette (5–500 μL) that is self-adjusting and very reproducible.

Langmuir, Irving (1881–1957), US physical chemist and inventor; Nobel Laureate in Chemistry (1932), for his discoveries and investigations in surface chemistry.

Langmuir adsorption isotherm an equation describing the fraction of the surface of an adsorbent covered with a monomolecular layer of an adsorbed gas, arrived at from a consideration of the number of gas molecules striking and leaving the surface in a given time. It is:

$$V/V_m = k_1p/(1 + k_2p),$$

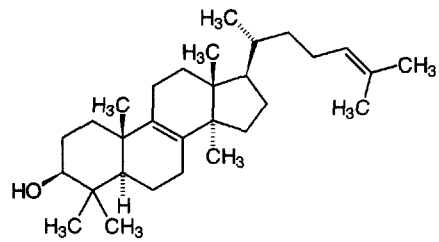
where V is the volume of gas adsorbed, V_m is the volume of gas required to cover the whole surface, p is the gas pressure, and k_1 and k_2 are constants for the system. *Compare* **Hill–Langmuir equation**.

Langmuir–Blodgett multilayer a thin film of oriented amphiphilic molecules, consisting of superposed monolayers built up by successive dipping and withdrawing of a solid substrate, e.g. a glass slide, through an insoluble monolayer of an appropriate amphiphilic substance (or mixture of such substances) spread on the surface of an aqueous solution and kept at constant pressure. [After I. Langmuir and Katharine B. Blodgett (1898–1979).]

Langmuir trough an apparatus for measuring the dependence of the surface force exerted by a film of a substance (of low vapour pressure), floating on a liquid with which it is immiscible, on the area of the film. The apparatus consists of a rectangular tank containing the subnatant liquid, e.g. water, on which a known amount of the immiscible substance, e.g. an oil or a higher fatty acid, is spread between two parallel barriers to form a film. One of the barriers is fixed and the other may be moved so as to compress the film to a predetermined area. The force exerted on the film to achieve any given area is measured by a system of levers and either a torsion wire or balancing masses.

lanolin *or* **wool fat** the fatlike secretion of the sebaceous glands of sheep that is deposited onto the wool fibres. It is a wax consisting of a complex mixture of esters and polyesters of over 30 high-molecular-mass aliphatic, steroid, and triterpenoid alcohols and a similar number of fatty acids. Lanolin normally contains 25–30% water and is widely used as an ointment base. *See also* **lan+**.

lanosterol kryptosterol; lanosta-8,24-dien-3β-ol; a steroid alcohol (triterpene) originally obtained from **lanolin**. It occurs in the biosynthetic pathway from squalene 2,3-epoxide to cholesterol in animals and fungi, but not in photosynthetic tissues, where it is replaced by **cycloartenol**. *See also* **lanosterol synthase**.



lanosterol

lanosterol synthase EC 5.4.99.7; *other names*: 2,3-epoxysqualene–lanosterol cyclase; oxidosqualene–lanosterol cyclase (*abbr.*: OSC); an enzyme of the pathway for the synthesis of sterols. It catalyses the cyclization of (*S*)-2,3-epoxysqualene to lanosterol. Example from *Saccharomyces cerevisiae*: database code ERG7_YEAST, 730 amino acids (83.33 kDa).

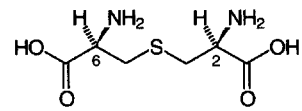
lantern *see* **firefly lantern**.

lanthanoid *or* **lanthanide** *or* (*formerly*) **lanthanon** any member of the series of 15 metallic elements with atomic numbers 57 (lanthanum) to 71 (lutecium) inclusive that occur together in group 3 and period 6 of the IUPAC **periodic table**; sometimes the term is restricted to the 14 elements following lanthanum. Lanthanoid is now the preferred name. Together with the elements scandium and yttrium, the lanthanoids are known also as **rare-earth elements** *or* (*more loosely*) **rare earths** (the latter term referring strictly to their oxides). Despite such names, however, they do mostly occur widely in nature, albeit in small amounts. Apart from the element of atomic number 61 (promethium), all lanthanoids have at least one stable nuclide and occur naturally, the principal source being the mixed phosphate ore monazite. All nuclides of promethium, however, are radioactive, and (except for traces possibly occurring as a fission product of natural uranium) all are artificial. The lanthanoids are strongly electropositive, and their chemical properties are similar, due usually to the filling of an inner electron subshell (4f) progressively across the series. Like the **actinoids**, they thus represent a series of inner transition elements within the series of **transition elements** embraced by groups 3 to 11 inclusive. Some paramagnetic lanthanoid ions induce strong shifts in the positions of many NMR spectral peaks and have been used as relaxation and shift probes in structural studies employing NMR spectroscopy.

lanthionine (2*S*,6*R*)-lanthionine, *meso*-lanthionine, *S*-(alanin-3-yl)-L-cysteine, 2,2′-diamino-3,3′-thiobis(propionic acid); *symbol* (recommended):

Ala
|
Cys

or Lan; a di(α-amino acid) found in **lantibiotic** polypeptides. It is formed as a post-translational modification, the first step involving dehydration of a Ser to the α,β-unsaturated amino-acid residue, 2,3-didehydroalanine. A bond is then formed between the $=CH_2$ group thus formed and the sulfur atom of a cysteine, inversion of configuration of the α carbon of the Ser-derived moiety occurring in the process. Chick embryo protein contains the (2*R*,6*R*) diastereoisomer. Lanthionine is also formed artefactually by the mild alkaline treatment of wool, hence its name (*see* **lan+**).



(2*S*,6*R*)-lanthionine

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lantibiotic any of a number of polypeptides, of 1.89–4.63 kDa, that contain **lanthionine** or methyllanthionine (*threo*-β-methyllanthionine, (2*S*,3*S*,6*R*)-3-methyllanthionine) and have antibiotic action. They are produced by and primarily act on Gram-positive bacteria. In addition to lanthionines, they contain the amino acids 2,3-didehydroalanine (*abbr.*: Dha) and 2,3-didehydrobutyrine (2-aminocrotonic acid, (*Z*)-2-aminobut-2-enoic acid, *abbr.*: Dhb) resulting from dehydration of serine and threonine residues respectively. These amino acids are formed post-translationally from normally coded amino acids. Lantibiotics are broadly divided into type A, elongated amphiphilic peptides, and type B, compact globular peptides. Type-A peptides kill bacterial cells by forming pores in the cytoplasmic membrane, type-B peptides possibly acting by enzyme inhibition.

LAP *(in clinical chemistry) abbr. for* leucine aminopeptidase (LAS preferred).

LA-PF4 *abbr. for* low-affinity platelet factor 4; a peptide derived from **platelet basic protein precursor**. It stimulates DNA synthesis, mitosis, glycolysis, intracellular cyclic AMP accumulation, prostaglandin E_2 secretion, and synthesis of hyaluronic acid and sulfated glycosaminoglycan. *Other name*: connective-tissue activating peptide III (*abbr.*: CTAP-III).

Laplace transform method a method that enables solutions of linear differential equations with constant coefficients to be found by reference to tables of Laplace transform pairs, with a minimum of mathematical work. The Laplace transform of a function $y = F(t)$ is defined by:

$$F(s) = \int_0^\infty e^{-st}F(t)\mathrm{d}t$$

in which s is usually a complex quantity and must have a positive real term, so that e^{-st} will be zero when $t = \infty$. [After Pierre Simon, Marquis de Laplace (1749–1827), French astronomer and mathematician.]

Largactil *see* **chlorpromazine**.

large calorie *an alternative name for* **kilocalorie** *or* (*in nutrition*) **Calorie**.

large-patch repair (of DNA) *a name sometimes given to* the process of excision repair of duplex DNA in some mutant organisms, e.g. *polA*⁻ *Escherichia coli*, in which the newly synthesized polynucleotide 'patch' is considerably larger than in the wild type.

large T-antigen *see* **T antigen** (def. 1).

lariat a lasso-shaped structure formed from the fragment of RNA to be excised during the process of splicing out the introns in the primary transcript of eukaryotic genes.

lariat debranching enzyme an enzyme that cleaves the 2′,5′-phosphodiester bond formed during pre-mRNA splicing between the 5′-terminal guanylyl residue of the intron and an adenylyl residue near the 3′ splice site, at the branch point of excised intron lariats. It is involved in the turnover of excised introns. Example from yeast: database code DBR1_YEAST, 405 amino acids (47.69 kDa).

Larmor frequency the angular frequency of **Larmor precession** of an atomic electron.

Larmor precession the **precession** of a charged particle moving under the influence of a central force, e.g. of an orbiting electron in an atom, when acted on by an external magnetic field. [After Joseph Larmor (1847–1942), Irish-born physicist.]

LAS *(in clinical chemistry) abbr. for* leucine aminopeptidase (preferred alternative to LAP).

lasalocid *or* **X-537A** any of five closely related lipophilic antibiotics, lasalocid A–E, isolated from cultures of *Streptomyces lasaliensis*. Lasalocid A ($M_r = 591$) is a carboxylic ionophore for virtually every known cation, but transports monovalent cations about ten times more effectively than divalent cations.

lased light *an imprecise term for* laser light; *see* **laser** (def. 2).

laser 1 any device for producing an intense, coherent, monochromatic, parallel beam of light (or other electromagnetic radiation) by stimulated emission. A laser consists of an optically transparent cylinder containing an active medium bounded by a full mirror at one end and by a partial mirror at the other end. Some chemical species of the medium are excited above their ground state by application of electromagnetic radiation from an external source; the excited species revert to their ground state with the emission of a photon, which in turn can collide with other excited species to produce stimulated emission of other photons. The radiation is reflected backwards and forwards up and down the cylinder and the beam emerges through the partial mirror. The frequency of the radiation is determined by the nature of the active medium; many different types of laser are available with a wide range of power outputs. **2** having the characteristic quality of, being, or using, light emitted by a **laser** (def. 1), as in laser densitometry, laser ionization (micro) mass spectrometry, laser light, laser microprobe mass analysis, laser nephelometry, laser photolysis, laser (light) scattering, laser spectrophotometry, and laser velocimetry. [Acronym from light amplification by stimulated emission of radiation.]

Latapie mincer a device for mincing tissues for metabolic studies in which both the rate of rotation of the cutting disks and the rate at which the tissue is forced against these disks may be controlled by varying the rates at which two cranks are turned, thus enabling minces of different degrees of fineness to be obtained. Sterile conditions may be maintained during the mincing if desired.

late enzyme *see* **late gene**.

late gene any gene of a bacteriophage or other viral genome that is expressed significantly, as a **late enzyme** or other **late protein**, only after replication of the genome has started. *Compare* **early gene**.

latency 1 *or* **crypticity** the state or quality of being **latent**. **2** *an alternative term for* **latent period**.

latent 1 existing in a potential, dormant, or suppressed form but usually capable of being expressed or evoked. **2** *(in pathology)* (of an infection or disease) not yet manifest or apparent.

latent enzyme any enzyme whose activity only becomes manifest when the conditions are changed. The term is used especially of a particulate enzyme that becomes active when the particles are disrupted.

latent heat *symbol*: *L*; the change in the heat content of a (given amount of) substance when it changes phase without change in its temperature.

latent image *(in photography)* the invisible image produced by the action of light, etc. on the photosensitive emulsion that is made visible by development.

latent period *or* **latency** 1 the time between the arrival of a stimulus at an irritable tissue and the beginning of the appropriate response. **2** the time between the adsorption of virulent bacteriophage onto a bacterium and lysis with liberation of newly formed virions.

late protein *see* **late gene**.

lateral phase separation the phenomenon of coexistence of solid and liquid regions in a lipid bilayer at temperatures between the **pretransition temperature** and the **transition temperature**.

lathyrism any of several pathological states that result from ingesting any of several toxins, characteristically found in plants of the genus *Lathyrus*. In humans one kind of lathyrism is characterized by a spastic paraplegia of the lower extremities associated with degenerative changes in the lateral pyramidal tracts of the spinal cord. It is caused by ingestion of neurotoxins, e.g. β-cyano-L-alanine and L-α,γ-diaminobutyric acid. These are present in several species of plants of the genus *Lathyrus* and in the common vetch (*Vicia sativa*). In experimental animals a defect of cross-linking of collagen is caused by feeding sweet pea (*Lathyrus odoratus*) seeds; the toxic substance was first identified as β-(γ-L-glutamyl)aminopropionitrile but it was later shown that β-aminopropionitrile alone is fully active. Turkeys fed *L. odoratus* died of hemorrhage from rupture of the aorta.

lathyrogen any member of a group of substances that on ingestion induce the disease **lathyrism**.

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Latin square *(in statistics)* a square array of n columns and n rows containing n different elements and in which no element occurs more than once in any row or column. It is used as a basis of experimental procedures when it is desired to allow for two sources of variability while investigating a third.

LATS *abbr. for* long-acting thyroid stimulator.

lattice **1** any regular array of objects or points in two or three dimensions. **2** *(in crystallography)* any regular, three-dimensional array of fixed points about which atoms, ions, or molecules vibrate in a crystal. **3** *(in immunology)* the three-dimensional aggregate suggested to be built up in an antigen–antibody reaction (*see* **lattice hypothesis**).

lattice energy (of a crystal) the energy that would be required to separate the ions of a crystal to an infinite distance from each other.

lattice hypothesis a hypothesis describing antigen–antibody reactions in terms of the building up of large antigen–antibody aggregates or three-dimensional lattices. The hypothesis requires both antigen and antibody to have valencies greater than one.

Lau *symbol for* the dodecanoyl (i.e. **lauroyl**) group.

Laue, Max Theodor Felix von (1879–1960), German physicist, Nobel Laureate in Physics (1914) 'for his discovery of the diffraction of X-rays by crystals'.

Laue equation any of a set of three equations describing the occurrence, positions, and intensities of X-ray beams after diffraction by a crystal. For three crystal axes, x, y, and z, with separations of chemical entities along them of a, b, and c, respectively, the equations are:

$$a(\cos\alpha - \cos\alpha_0) = h\lambda,$$

$$b(\cos\beta - \cos\beta_0) = k\lambda,$$

and

$$c(\cos\gamma - \cos\gamma_0) = l\lambda,$$

where α_0, β_0, and γ_0 are the angles that the incident beam makes with the x, y, and z, axes, respectively, and α, β, and γ are the corresponding angles for the diffracted beam; λ is the wavelength of the radiation and h, k, and l are integers corresponding to the **Miller indices** of the planes considered to be diffracting the radiation. *See also* **Bragg's law**. [After M. F. T. von **Laue**.]

Laue photograph *or* **Laue pattern** the spot diagram produced when a heterogeneous beam of X-rays is diffracted by passage through a crystal.

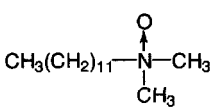
laurate **1** *the trivial name for* dodecanoate, CH_3–$[CH_2]_{10}$–COO^-, the anion derived from lauric acid (i.e. dodecanoic acid), a saturated straight-chain higher fatty acid. **2** any mixture of free lauric acid and its anion. **3** any salt or ester of lauric acid. Dodecyl laurate is one of the main components of laurel oil, the oil obtained from berries of the laurel plant, *Laurus nobilis*. Laurate is present in appreciable amounts in hydrolysates of phosphoglycerides of plants and animals.

Laurell technique *an alternative name for* **rocket immunoelectrophoresis**. [After C.-B. Laurell, Swedish biochemist.]

lauroyl *or (formerly)* **lauryl** *symbol*: Lau; *the trivial name for* dodecanoyl, CH_3–$[CH_2]_{10}$–CO–, the acyl group derived from lauric acid (i.e. dodecanoic acid). It occurs in natural lipids, mainly as acylglycerols.

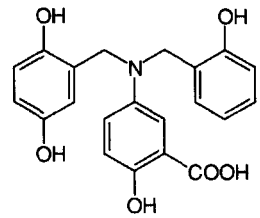
lauryl **1** *symbol*: Dod; *a common name for* dodecyl, CH_3–$[CH_2]_{10}$–CH_2–, the alkyl group derived from dodecane; use deprecated. **2** *a former trivial name for* dodecanoyl (lauroyl now used).

lauryldimethylamine oxide *abbr.*: LDAO; *N*,*N*-dimethyl-*N*-dodecylamine oxide; a water-soluble, zwitterionic (at pH 7 or above) detergent, aggregation number 76, CMC 1–2 mM.



lauryl sulfate, sodium salt *an alternative name for* **sodium dodecyl sulfate**.

lavendustin any of several substituted amino salicylic acids that are used as protein tyrosine kinase inhibitors. Lavendustin A is {5-amino-[(*N*-2,5-dihydroxybenzyl)-*N*′-2-hydroxybenzyl]}aminosalicylic acid and lavendustin C is 5-(*N*-2,5-dihydroxybenzyl)aminosalicylic acid. Lavendustin A inhibits protein tyrosine linase activity with little effect on cyclic AMP-dependent kinase or protein kinase C. Lavendustin C is similar but also inhibits Ca^{2+}/calmodulin kinase II.



lavendustin A

lawn a layer of microorganisms uniformly distributed in or over the surface of a solid culture medium.

law of conservation of energy *see* **thermodynamics, laws of**.

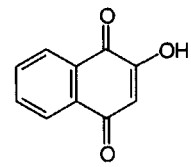
law of independent assortment *see* **Mendel's laws of heredity**.

law of mass action *see* **mass action**.

Lawrence, Ernest Orlando (1901–58), US physicist; Nobel Laureate in Physics (1939) 'for the invention and development of the cyclotron and for results obtained with it, especially with regard to artificial radioactive elements'.

laws of thermodynamics *see* **thermodynamics**.

lawsone 2-hydroxy-1,4-naphthoquinone; the active dyeing compound of **henna**.



layer line one of the parallel lines of spots obtained on the photographic plate in the rotating crystal method of X-ray diffraction analysis.

lb *symbol for* pound.

LBF *abbr. for Lactobacillus bulgaricus* factor (*see* **pantetheine**).

LC *abbr. for* liquid chromatography.

LCAD *abbr. for* long-chain acyl-CoA dehydrogenase; *see* **beta-oxidation system**.

LCAT *abbr. for* lecithin–cholesterol acyl transferase.

LCD *abbr. for* liquid-crystal display.

L cell *an alternative name for* **EG cell**.

L chain *see* **light chain** (def. 1).

LCK a gene family encoding nonreceptor tyrosine kinases (e.g. $p56^{lck}$) of the Src family (*see* ***src***), originally detected in the LSTRA murine lymphoma cell line. The product is lymphocyte-specific and associates with the cytoplasmic domains of CD4 and CD8. The mitogen-activated protein (MAP) kinase is a substrate for $p56^{lck}$; it is a myristoylated protein with SH2 and SH3 domains. Example from human: database code KLSK_HUMAN, 508 amino acids (57.80 kDa).

LCR *abbr. for* locus control region.

LD *abbr. for* **1** lethal dose. **2** *(in clinical chemistry)* L-lactate dehydrogenase (alternative to LDH); *see also* **HBD**. **3** low density.

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LD_{50} *abbr. for* median lethal dose.
LDH *abbr. for* L-lactate dehydrogenase (alternative to LD).
LDL *abbr. for* low-density lipoprotein.
LDL receptor a cell-surface receptor that binds apolipoprotein B and so internalizes **low-density lipoprotein** (LDL) from the plasma, leading to processing that regulates cholesterol and LDL synthesis, and thence plasma cholesterol concentration. It is a type I membrane protein. The number of LDL receptors on liver cells is regulated by cholesterol synthesis: when cholesterol levels rise, the number of receptors falls. Defects in this receptor are associated with certain forms of type II **hyperlipidemia**. The amino end of the extracellular domain contains seven or eight 40-residue repeats; each repeat has about six Cys residues, all of which are involved in disulfide bonds; following these repeats is a region of about 350 residues that is homologous with part of the epidermal growth factor precursor. Example (precursor) from human: database code LDLR_HUMAN, 860 amino acids (95.27 kDa).
Le *abbr. for* Lewis antigen.
leaching (microbial) a process for the solubilization of metals, mostly from poor ores, by lithotrophic bacteria. *See also* **lithotroph**.
lead *symbol*: Pb; a very soft, bluish-white metallic element of group 14 of the IUPAC **periodic table**. It has a low melting point and high relative density; proton number 82; relative atomic mass 207.2. It is commonly used for shielding from ionizing radiation.
leader peptidase EC 3.4.99.36; *other name*: signal peptidase I, phage-procoat-leader peptidase; an enzyme that catalyses the cleavage of N-terminal leader sequences from secreted proteins.
leader peptide *an alternative name for* **signal peptide**.
leader sequence *or* **lead sequence** *an alternative name for* signal sequence (*see* **signal peptide**).
leading strand the DNA strand that is synthesized continuously, in the 5′ to 3′ direction, towards the replication fork during the discontinuous replication of duplex DNA. *Compare* **lagging strand**.
lead screw a threaded rod the rotation of which is used to drive the tool carriage of a lathe, the plunger of a syringe, etc.
leaf (*pl.* **leaves**) **1** the principal organ of photosynthesis and transpiration in higher plants. It typically consists of a flattened bladelike lamina, often relatively broad, attached to the plant stem directly or by a stalk. **2** any thin, flattened object that resembles a leaf. *See also* **leaflet**.
leaflet **1** **a** any small or young **leaf** (def. 1). **b** an individual segment of a compound leaf. **2** any small, thin, flattened object or structure that resembles the leaf of a plant, especially a lipid bilayer or a portion of a biological membrane.
leaky *(in genetics)* describing any mutation that fails to shut off completely the activity of a gene so that some residual expression of the gene remains.
Le antigen *symbol for* Lewis antigen.
least squares a statistical method for determining the 'best' value of an unknown quantity relating one or more sets of measurements or observations. It is based on minimizing the sum of the squares of the deviations of the experimentally determined values from the calculated values, and is used especially to find a curve that best fits a given set of data.
leaving group any atom or group, charged or uncharged, that departs during a substitution or displacement reaction from what is regarded as the residual or main part of the substrate of the reaction.
Lebedev-Saft *or* **Lebedev juice** an aqueous extract of air-dried yeast. It will ferment glycerone (dihydroxyacetone) and, in the presence of phosphate, produces a hexose phosphate. [After Alexander Nikolaevich Lebedev (1881–1938), Russian botanist who described the preparation in 1911.]
Le Chatelier principle *or* **Le Chatelier–Braun principle** a principle stating that when a system in equilibrium is subject to stress, i.e. to a change in its conditions, the system will adjust itself to annul, as far as possible, the effect of the stress. [First formulated (in 1885) by Henry (Louis) Le Chatelier (1850–1936), French chemist, and independently in 1886 by Karl Ferdinand Braun (1850–1918), German physicist.]
lecithin *an old trivial name, still in frequent use, for* any 3-*sn*-**phosphatidylcholine**.
lecithinase any of a number of distinct enzymes acting on lecithins that are now usually considered among the **phospholipases**.
lecithin-cholesterol acyl transferase *abbr.*: LCAT; EC 2.3.1.43; *recommended name*: phosphatidylcholine-sterol *O*-acyltransferase; *other name*: phospholipid–cholesterol acyltransferase. An enzyme that catalyses a reaction between phosphatidylcholine and cholestereol to form a cholesteryl ester and 1-acylglycerophosphocholine. This enzyme is central to the extracellular metabolism of plasma lipoproteins; it acts on free cholesterol in the high-density lipoprotein (HDL) precursor, transferring a fatty acyl group to cholesterol, thus contributing to the altered class composition of the mature HDL; some of the resulting cholesterol esters are partly taken up by low-density lipoprotein. The enzyme is a glycoprotein, and is activated by apolipoprotein A1. It is deficient in Norum and fish eye diseases. Example (precursor) from human: database code LCAT_HUMAN, 440 amino acids (49.52 kDa).
lectin any of a group of specific agglutinins and other antibody-like (glyco)proteins of nonimmune origin, defined (by IUB) as 'sugar-binding protein or glycoprotein of non-immune origin which agglutinates cells and/or precipitates glycoconjugates'. Lectins are widely distributed in nature, being found mainly in seeds but also in other parts of certain plants, and in many other organisms from bacteria to mammals. Lectins bear at least two sugar-binding sites; they bind specific sugars and thereby precipitate certain polysaccharides, glycoproteins, and glycolipids, and/or agglutinate animal and plant cells. Some can distinguish between normal and malignant cells, and many, e.g. phytohemagglutinin, are mitogenic. They are widely used experimentally, especially **concanavalin A**, as tools in carbohydrate biochemistry, for studying cell surfaces and for inducing **transformation** (def. 3) of lymphocytes. Plant lectins are also known as **phytoagglutinins**.
LED *abbr. for* light-emitting diode.
Lederberg, Joshua (1925–), US geneticist notable for his work on sex factors in bacteria and for discovering bacterial transduction; Nobel Laureate in Physiology or Medicine (1958) 'for his discoveries concerning genetic recombination and the organization of the genetic material of bacteria' [prize shared with G. W. Beadle and E. L. Tatum].
leghemoglobin *or (esp. Brit.)* **leghaemoglobin** a hemoglobin-like red pigment found in the root nodules of leguminous plants. An autoxidizable hemoprotein, it sequesters dioxygen to prevent inhibition of **nitrogenase** in the bacteroids. It is thus essential for symbiotic nitrogen fixation. Example, leghemoglobin I (monomer) from pea: database code LGB1_PEA, 147 amino acids (15.82 kDa).
legumain EC 3.4.22.34; *other names*: bean endopeptidase; vicilin peptidohydrolase; phaseolin; an endopeptidase from legumes that hydrolyses Asn-|-Xaa bonds in small molecule substrates such as Boc-Asn-|-$OPhNO_2$. Example (precursor) from *Phaseolus vulgaris*: database code CYSP_PHAVU, 362 amino acids (40.17 kDa).
legumin a major storage protein of the seeds of both leguminous and nonleguminous plants. It consists of two chains, an acidic α chain and a basic β chain which are linked by a single disulfide bond. These are derived from a common precursor; example (precursor) from *Pisum sativum*: database code LEG2_PEA, 520 amino acids (59.27 kDa). Residues 23–335 form the α chain, and 336–520 the β chain.
Leigh theory a theory that enables the use of electron spin resonance data to estimate distances between two interacting spins embedded in a rigid lattice. [After J. S. Leigh.]
Leloir, Luis Federico (1906–87), Argentinian biochemist noted

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for his isolation of uridine diphosphate glucose and his discovery of the role of sugar nucleotides in interconversion of sugars and in polysaccharide formation; Nobel Laureate in Chemistry (1970) 'for his discovery of sugar nucleotides and their role in the biosynthesis of carbohydrates'.

LEM *abbr. for* light-effect mediator.

length *symbol*: *l or L*; a scalar physical quantity indicating linear extent; one of the seven SI base physical quantities. The SI base unit of length is the **metre**.

lens **1** a piece of glass or other transparent and refracting material, or two or more such pieces joined together, for converging or diverging a beam of light in order to form optical images. **2** any electrostatic or electromagnetic device for focusing or otherwise altering the direction of movement of a beam of electrons or other elementary charged particles; any similar device acting on sound waves. **3** *(in zoology)* any of various transparent structures responsible for focusing light onto photoreceptors. The **crystalline lens** of vertebrates is a near-spherical structure in the eye, lying in the aqueous humour behind the pupil. It focuses or assists in focusing light rays onto the retina. Enclosed within a collagenous capsule, it consists largely of cells containing proteins called **crystallins**.

lenticular **1** having the shape of a biconvex **lens** (def. 1). **2** of or pertaining to a **lens**.

lentinan a polysaccharide isolated from the edible mushroom *Lentinus edodes*. It is a β-1,3-glucan, having for every five β-1,3 linear linkages, two glucopyranoside units in β-1,6 linkage.

lentinarin *see* **callose**.

lentropin a protein, present in the vitreous humour of the eye, that stimulates lens-fibre differentiation. It is related to **insulin-like growth factors**.

Lepidoptera a large order of insects that includes butterflies, skippers, and moths. The adults are characterized by a prominent coiled proboscis and two pairs of large, scaly, membranous wings. The larvae are caterpillars. —**lepidopteran** *adj.*

leporine of, pertaining to, or resembling a rabbit or hare.

leprachaunism an autosomal recessive inherited disease characterized by small stature and elfin-like appearance, with motor and mental retardation and severe failure to thrive. Most patients die in early childhood, though a few, who are compound heterozygotes for two different alleles, survive childhood. The condition can be caused by any of a number of mutations in the gene encoding the insulin receptor. These involve changes in single amino acids, those so far found being between residues 55 and 487.

leptin a protein encoded by a gene, *ob*, first identified as the *obese* mutation (*see* ***ob/ob***) in mice. Leptin may act as a signal in the regulation of adipose mass, possibly by regulating appetite and also possibly by regulating energy expenditure. It appears to be expressed exclusively in white adipose tissue. The predicted sequence is largely hydrophilic and has structural features indicative of a secreted protein. Example from human (precursor): database code OB_HUMAN, 167 amino acids (18.64 kDa). *See also* **leptin receptor**.

leptin receptor a receptor family that binds **leptin** and is presumed to mediate its intracellular effect. It is probably encoded by the gene *db* (for *diabetes*), and has at least six alternatively spliced forms. It is expressed at high levels in the hypothalamus relative to other tissues. A mutant form of the receptor which lacks the cytoplasmic region is likely to be defective in signal transduction and may be responsible for obesity in *db* mice. Example from human (precursor): database code OBR_HUMAN, 1165 amino acids (132.45 kDa). *See also* **diabetes mutation**, ***ob/ob***.

leptocene the first phase of prophase I in **meiosis**.

leptotene *see* **meiosis**.

Lesch–Nyhan syndrome an X-chromosome-linked, inherited disorder of male humans in which there is an almost complete deficiency of **hypoxanthine phosphoribosyltransferase** (EC 2.4.2.8), one of the two key enzymes of the **salvage pathway** of purine metabolism. Clinically the condition is characterized by hyperuricemia, excessive uric-acid biosynthesis, and certain neurological features including self-mutilation, spasticity, and mental retardation. Death usually occurs in the second or third decade of life. [After M. Lesch (1939–) and William Leo Nyhan (1926–), US physician and biochemist.]

lesion **1** *(in pathology)* a zone of tissue with impaired function resulting from damage by disease or wounding. **2** *(in biochemistry)* any deleterious disturbance of a metabolic pathway resulting from chemical interference or genetic abnormality.

+less *suffix forming adjectives and adverbs* without, lacking; unable to do or to be done. In biochemistry it is used especially of auxotrophic mutants to indicate the substance they cannot synthesize, e.g. thymineless mutant.

let23 a gene in *Caenorhabditis elegans* for a receptor **tyrosine kinase** of the epidermal growth factor family. It is probably activated by the ***lin3*** product. The product of *let23* is a type I membrane glycoprotein. Precursor: database code LT23_CAEEL, 1323 amino acids (150.34 kDa).

lethal dose *abbr.*: LD; the amount of a drug or other agent that when administered to an organism causes the organism's death. *See also* **median lethal dose**.

lethal factor any **lethal mutation**.

lethal gene any gene carrying a **lethal mutation**. Such mutations may only be fatal in the homozygous state.

lethal mutant any organism carying a **lethal mutation**.

lethal mutation any **mutation** that may bring about the death of the organism before its maturity. The consequences of such a mutation may depend on whether the organism is homozygous or heterozygous for the gene in question, and possibly also on the conditions (*see* **conditional lethal mutation**).

lethal synthesis any process by which a highly toxic compound is synthesized in an organism from a nontoxic precursor. The classic example is the formation of **fluorocitrate** when e.g. kidney homogenates are incubated with **fluoroacetate**. The fluorocitrate thus formed inhibits **aconitase**.

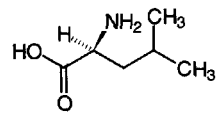
LETS protein *abbr. for* large external transformation sensitive (glyco)protein (i.e. cellular **fibronectin**).

Leu *symbol for* a residue of the α-amino acid L-leucine (alternative to L).

leuc+ *a variant spelling of* **leuk+**. *See* **leuko+**.

leucinate **1** leucine anion; the anion, $(CH_3)_2CH–CH_2–CH(NH_2)–COO^-$, derived from **leucine**. **2** any salt containing leucine anion. **3** any ester of leucine.

leucine *the trivial name for* α-aminoisocaproic acid; α-amino-γ-methylvaleric acid; 2-amino-4-methylpentanoic acid; $(CH_3)_2CH–CH_2–CH(NH_2)–COOH$; a chiral α-amino acid. L-leucine (*symbol*: L *or* Leu), (*S*)-2-amino-4-methylpentanoic acid, is a coded amino acid found in peptide linkage in proteins; codon: CUA, CUC, CUG, or CUU; UUA or UUG. In mammals it is an essential amino acid and is ketogenic. Residues of D-leucine (*symbol*: D-Leu *or* DLeu), (*R*)-2-amino-4-methylpentanoic acid, occur in a number of peptide antibiotics, e.g. gramicidins A, B, C, and D and polymixins D_1, D_2, E_1, and E_2.



L-leucine

leucine aminopeptidase *abbr. (in clinical chemistry)*: LAP (preferred) *or* LAS; *the common name for* aminopeptidase (cytosol) (EC 3.4.11.1), an enzyme that, despite its name, in fact acts on most amino-acid residues. It is widely distributed in animal tissues, its level in the serum being useful clinically in monitoring hepatobiliary disease processes and placental well-being. The recommended name is leucyl aminopeptidase.

leucine and valine biosynthesis the biosynthesis of leucine

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and valine initially follows a common pathway that commences with the formation of acetolactate from two molecules of pyruvate, a reaction catalysed by acetolactate synthase. Acetolactate is converted via α,β-dihydroxyisovalerate (2,3-dihydroxy-3-methylbutanoate) to α-ketoisovalerate (2-oxo-3-methylbutanoate). At this point the pathway branches. α-Ketoisovalerate can be converted by transamination with glutamate to valine. Alternatively, it can be converted successively to α-isopropylmalate (2-isopropylmalate), β-isopropylmalate (3-isopropylmalate), and α-ketoisocaproate (4-methyl-2-oxopentanoate), and thence by transamination with glutamate to leucine. *See also* **3-isopropylmalate dehydratase**, **3-isopropylmalate dehydrogenase**.

[5-leucine]enkephalin *abbr.*: [Leu^5]enkephalin *or* [Leu]-enkephalin; *the recommended trivial name for* the pentapeptide Tyr-Gly-Gly-Phe-Leu. *See* **enkephalin**.

leucine-rich repeat *abbr.*: LRR; short sequence motifs in proteins, of average length 24 residues, containing a high proportion of leucines, typically five to seven at positions 2, 5, 7, 12, 16, 21, and 24 within the repeat. Such arrays form an amphipathic sequence, with leucine as the predominant hydrophobic residue. It is thought they participate in protein–protein or protein–lipid interaction. The first was discovered in α_2-glycoprotein, but they have since been found in other proteins. The number of such repeats can vary from one, in platelet glycoprotein Ibβ to 30, in e.g. **chaoptin**. Structure analysis has shown that in ribonuclease inhibitor protein these repeats comprise 90% of the protein, and that they correspond to β–α structural units, arranged to form a parallel β sheet with a parallel α helix, such that the β sheet has one surface exposed to solvent so that the protein acquires a non-globular shape.

leucine zipper a set of leucines (normally four or five) repeating every seventh amino-acid residue in a protein structure. Such an arrangement was originally found in DNA-binding proteins, but it is now known to occur also in other proteins, especially adjacent to proposed transmembrane regions, mediating dimerization. The abbreviation ZIP is used e.g. in designating the **bZIP** family of proteins. *See also* **potassium channels**.

leucinium leucine cation; the cation, $(CH_3)_2CH–CH_2–CH(NH_3^+)–COOH$, derived from **leucine**.

leucino the alkylamino group, $(CH_3)_2CH–CH_2–CH(COOH)–NH–$, derived from **leucine**.

leuco+ *a variant spelling of* **leuko+**.

leucocyte *a variant spelling of* **leukocyte**.

leucyl the acyl group, $(CH_3)_2CH–CH_2–CH(NH_2)–CO–$, derived from **leucine**.

leucyl aminopeptidase EC 3.4.11.1; *other names*: leucine aminopeptidase; peptidase *S*; cytosol aminopeptidase; an enzyme that catalyses the hydrolysis of an aminoacyl-peptide to an amino acid and the residual peptide. It thus releases the N-terminal amino acid of a protein, provided the amino group is free; it has been so used in protein sequence determination. Its action is most rapid when the N-terminal amino acid is leucine; it liberates other residues at varying rates, and acts poorly at an Xaa-Pro bond. It requires zinc. Example from *Rickettsia prowazekii*: AMPL_RICPR, 500 amino acids (53.94 kDa).

[Leu^5]enkephalin *or* **[Leu]enkephalin** *abbr. for* [5-leucine]-enkephalin.

leuk+ *a variant form of* **leuko+** (before a vowel).

leukemia *or (esp. Brit.)* **leukaemia** *or (sometimes)* **leukosis** any of a group of neoplastic diseases of the leukocytes, usually involving increase in the number of leukocytes in the blood. Leukemias are classified according to the type of leukocyte affected and whether the disease is acute or chronic.

leukemia inhibitory factor *abbr.*: LIF; *also called* **differentiating-stimulating factor** *or* **differentiation-inducing factor**; a **cytokine** produced by fibroblasts, T cells, and macrophages. It is a monomer of 179 amino acids that maintains the pluripotent phenotype of embryonic stem cells, and potentiates interleukin-3-dependent proliferation of hemopoietic progenitors.

leuko *or* **leuco** describing the colourless derivative formed reversibly from a coloured substance, often by reduction; e.g. leuko compound, leuko dye.

leuko+ *or* **leuco+** *or (before a vowel)* **leuk+** *or* **leuc+** **1** white or colourless. **2** denoting of, pertaining to, or acting upon a leukocyte or leukocytes.

leukocidal *or* **leucocidal** describing an agent that kills leukocytes.

leukocidin *or* **leucocidin** any extracellular bacterial product that can kill leukocytes of certain animal species and that may also be toxic or lytic towards other cell types. Leukocidins are produced by pathogenic strains of *Staphylococcus* and *Streptococcus*.

leukocyte any white blood cell, i.e. one not containing an oxygen-transporting pigment such as hemoglobin. Vertebrate leukocytes include the **polymorphonuclear leukocytes**, **lymphocytes**, and **monocytes**; they are distinguished by size, shape, and staining characteristics. —**leukocytic** *or* **leucocytic** *adj.*

leukocytosis *or* **leucocytosis** a gross increase in the number of leukocytes in the blood. It often occurs as a response to an infection. *See also* **leukemia**.

leukokinin *or* **leucokinin** a specific cytophilic immunoglobulin G (IgG) obtained by fractionating human plasma IgG and constituting about 2% of the total IgG. It binds specifically and reversibly to autologous polymorphonuclear leukocytes, causing 2- to 2.5-fold stimulation of their phagocytic activity. A proteinase, **leukokininase**, cleaves from leukokinin a tetrapeptide, **tuftsin**, which is thought to bear all the activity.

leukopenia *or* **leucopenia** an abnormal decrease or deficiency of leukocytes circulating in the blood. *Also (esp. Brit.)* **leukopaenia** *or* **leucopaenia**.

leukoplast *or* **leucoplast** *or* **leukoplastid** *or* **leucoplastid** any of the colourless **plastids** found in plant cells. They include **aleuroplasts**, **amyloplasts**, and **elaioplasts**. Leukoplasts may develop into **chloroplasts**.

leukopoiesis *or* **leucopoiesis** the processes by which leukocytes are formed in the body. —**leukopoietic** *or* **leucopoietic** *adj.*

leukopterin *or* **leucopterin** 2-amino-4,6,7-trihydroxypteridine; a white pigment found in the wings of butterflies, especially white-winged butterflies.

leukosis *or* **leucosis** **1** a condition in which there is an abnormal proliferation of one or other of the leukocyte-forming tissues. **2** *an alternative name for* **leukemia**.

leukosulfakinin a sulfated myotropic 11-residue peptide isolated from head extracts of the cockroach. It exhibits sequence homology with human gastrin II and cholecystokinin.

leukotaxin *or* **leucotaxin** a nitrogen-containing material, found in injured tissue, that when injected into an animal causes increased capillary permeability and migration of leukocytes to the site of injection.

leukotoxin *or* **leucotoxin** **1** any compound toxic to leukocytes. **2** cytochrome P450-derived linoleic acid peroxide; any of a group of substances observed in high concentrations in burned skin samples that may have a bacteriocidal function. **Leukotoxin A** is (12*Z*)-9,10-epoxyoctadec-12-enoic acid, and **leukotoxin B** is (9*Z*)-12,13-epoxyoctadec-9-enoic acid (*abbr.*: EpODE) or, its methyl ester (*abbr.*: EpOME).

leukotriene *abbr.*: LT; any member of a family of pharmacologically active substances derived from polyunsaturated fatty acids, notably arachidonic acid, some of which contain a peptide moiety based on cysteine. They may be regarded as local hormones that are not stored, but synthesized in response to specific stimuli. They are formally derived from eicosanoic acid and contain a set of three conjugated double bonds (hence 'triene'); one or two additional double bonds, not conjugated to the others, may also be present – a subscript numeral after the abbreviation indicates the total number of double bonds, depending on the polyunsaturated fatty acid from which each is derived, e.g. LTA_4 from arachidonic acid, LTB_5 from eicosapentaenoic acid. They are products of the 5-lipoxygenase pathway. LTC_4 consists of glutathione linked to

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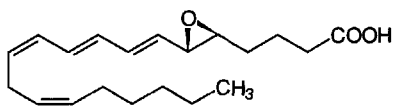
an eicosanoid; loss of glutamic acid from this leads to LTD_4, and loss of glycine then leads to LTE_4. These three, sometimes collectively known as **peptidoleukotrienes**, are potent spasmogenic agents that make up the active components of **slow-reacting substance of anaphylaxis** (SRS-A). *See also* individual entries below.

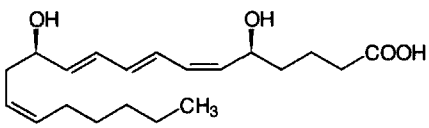
leukotriene A *abbr.*: LTA; any of a group of **leukotrienes** characterized as unstable 5,6-epoxides. Leukotriene A_4 (*abbr.*: LTA_4) is (7*E*,9*E*,11*Z*,14*Z*)-(5*S*,6*S*)-5,6-epoxyeicosa-7,9,11,14-tetraen-1-oate. Leukotriene A_3 (*abbr.*: LTA_3) is similar, but lacks the double bond at the C-14, while leukotriene A_5 (*abbr.*: LTA_5) has an additional, 17*Z*, double bond. LTA_4 is derived biosynthetically from arachidonate via 5-hydroperoxyeicosatetraenoate, and is the precursor either of leukotriene B_4 (*see* **leukotriene B**) by the action of highly specific **leukotriene-A_4 hydrolase** (EC 3.3.2.6), or of **leukotriene C_4** by the action of leukotriene-C_4 synthase (EC 2.5.1.37).



leukotriene A_4

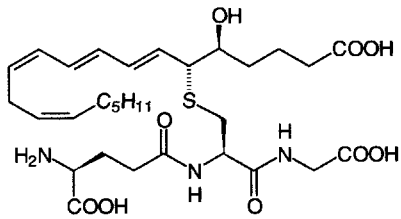
leukotriene-A_4 hydrolase *abbr.*: LTA_4 hydrolase; EC 3.3.2.6; an enzyme that converts (7*E*,9*E*,11*Z*,14*Z*)-(5*S*,6*S*)-5,6-epoxyeicosa-7,9,11,14-tetraenoate (LTA_4) to (6*Z*,8*E*,10*E*,14*Z*)-(5*S*,12*R*)-5,12-dihydroxyeicosa-6,8,10,14-tetraenoate (LTB_4). Example from human: database code LKHA_HUMAN, 610 amino acids (69.07 kDa).

leukotriene B *abbr.*: LTB; any of a group of **leukotrienes** characterized as (5*S*,12*R*)-5,12dihydroxy polyunsaturated acids. Leukotriene B_4 (LTB_4) is (6*Z*,8*E*,10*E*,14*Z*)-(5*S*,12*R*)-5,12-dihydroxyeicosa-6,8,10,14-tetraen-1-oate. Leukotriene B_5 (LTB_5) has an additional, 17*Z*, double bond. LTB_4 is a product of leukotriene-A_4 hydrolase (*see* **leukotriene A**); it is a major product of the 5-lipoxygenase pathway, and is a potent aggregatory, chemokinetic, and chemotactic agent for polymorphonuclear leukocytes (PMNLs) *in vitro* and induces increased vascular permeability and PMNL infiltration *in vivo*.



leukotriene B_4

leukotriene C_4 *abbr.*: LTC_4; a **leukotriene** comprising a glutathione moiety linked through its thio group to C-6 of an eicosanoid. LTC_4 is formed from LTA_4 and glutathione by leukotriene-C_4 synthase (EC 2.5.1.37). Among other actions, it is a potent mediator of smooth muscle contractility, and of vascular tone and permeability, being a potent vasoconstrictor in a variety of vascular beds including the coronary and cerebral circulations. It is the predominant leukotriene in the central nervous system.



leukotriene D_4 *abbr.*: LTD_4; a **leukotriene** comprising a cysteinylglycine moiety linked through its thio group to an eicosanoid moiety. It is a rapidly formed metabolite of **leukotriene C_4** (LTC_4), resulting from the action of membrane-bound γ-glutamyl transferase, which removes glutamic acid. Its actions are similar to those of LTC_4.

leukotriene E_4 *abbr.*: LTE_4; a **leukotriene** comprising a cysteine moiety linked to an eicosanoid moiety. It is derived metabolically from **leukotriene D_4** (LTD_4) by the action of specific membrane-bound dipeptidases, which remove glycine. It has a somewhat longer metabolic half-life than LD_4, but is further metabolized to a number of more polar products, notably those in which the terminal methyl group of the eicosanoid moiety is oxidized to a carboxyl group. It activates receptors in human airways and has been implicated in airway hyper-responsiveness in humans.

leukovirus *or* **leucovirus** any tumorigenic **retrovirus**.

leukovorin *or* **leucovorin** *see* **folinic acid**.

leumorphin an endogenous 29-amino-acid opioid peptide that corresponds to residues 228–256 of preproenkephalin B; the N-terminal 13 residues correspond to rimorphin (dynorphin B) and the N-terminal five to Leu-enkephalin (*see* **enkephalin**).

leupeptin any of several modified tripeptide protease inhibitors produced by various actinomycetes. Commonly *N*-acetyl-Leu-Leu-argininal is supplied for use in the laboratory; other variants have propionyl in place of acetyl, and valine or isoleucine in place of one or both leucines.

Leu-prolide an analogue of **gonadotropin-releasing hormone** in which residues 5 and 10 (glycine and glycinamide) are replaced by D-Leu and ethylamine respectively.

levan *a common name for* any (2→6)-β-D-fructofuranan; such compounds are produced mostly by bacteria. As in **inulin** each chain terminates in a (1→2)-α-D-glucopyranosyl residue, but it may also contain (2→1)-β branch points.

levansucrase *the recommended name for* sucrose 1-fructosyl transferase, EC 2.4.1.10; an enzyme that catalyses the reaction:

$$\text{sucrose} + (2,6\text{-}\beta\text{-D-fructosyl})_n = \text{glucose} + (2,6\text{-}\beta\text{-D-fructosyl})_{n+1}.$$

See also **sucrase** (def. 3).

levarterenol *see* **norepinephrine**.

levigate *(in chemistry)* **1** to grind (something) into a smooth powder or paste. **2** to separate fine from coarse particles by grinding and suspending them in a fluid. —**levigation** *n.*

Levi-Montalcini, Rita (1909–), Italian cell biologist; Nobel Laureate in Physiology or Medicine (1986) jointly with S. Cohen 'for their discoveries of growth factors'.

levo- *or (esp. Brit.)* **laevo-** *symbol*: *l*-; a prefix, no longer used, to denote a compound that is **levorotatory**; the levorotatory enantiomer of compound A is now designated as (–)-A.

levo+ *or (before a vowel)* **lev+** *comb. form* denoting on or towards the left. *Also (esp. Brit.)* **laevo+, laev+.** *Compare* **dextro+**.

levodopa *or (Brit.)* **laevodopa** (–)-3-hydroxy-L-tyrosine; a naturally occurring amino acid that has been used in the treatment of **Parkinson's disease** easing symptoms such as rigidity, postural problems, and slowness of movement. *See* **3,4-dihydroxyphenylalanine**.

levorotatory *or (esp. Brit.)* **laevorotatory** **1** *symbol*: (–)- *or (formerly) l*-; describing a chemical compound that rotates the plane of polarization of a transmitted beam of plane-polarized light or other electromagnetic radiation to the left, i.e. in an anticlockwise direction as viewed by the observer looking towards the light source. **2** describing any leftwards or anticlockwise rotation. *Compare* **dextrorotatory**. —**levorotation** *or* **laevorotation** *n.*

levorphanol 17-methylmorphinan-3-ol; a synthetic analogue of morphine. It is an orally active analgesic that binds stereo-

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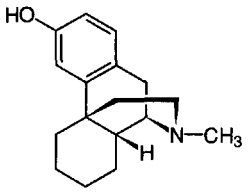
specifically with high affinity to opioid receptors (K_d 10^{-9} M). Five to six times more active than morphine, it is a controlled substance under the US Code of Federal Regulations. **Dextrorphan**, the dextrorotatory form, does not bind to opioid receptors, is not analgesic, but is a very effective antitussive.



levulose *or (esp. Brit.)* **laevulose** *an old name, still sometimes used in pharmacy, for* D-(−)-fructose, the levorotatory component of invert sugar. *Compare* **dextrose**.

Lewis acid any chemical species that is able to accept an electron pair and is thus able to react with a **Lewis base** to form an adduct (i.e. Lewis adduct). For example:

$$(CH_3)_3B + :NH_3 \rightarrow (CH_3)_3B^-N^+H_3$$

or

$$(CH_3)_3C^+ + Cl^- \rightarrow (CH_3)_3C{-}Cl;$$

i.e.

Lewis acid + Lewis base → Lewis adduct.

[After Gilbert Newton Lewis (1875–1946), US chemist.]

Lewis adduct the adduct formed between a **Lewis acid** and a **Lewis base**.

Lewis antigen *abbr.*: Le antigen; *symbol*: Le; one of the serologically distinguishable human **blood-group substances**. Lewis specificities are carried on glycosphingolipids and glycoproteins. Primarily a system of soluble antigens in secretions (e.g. saliva) and plasma, the Lewis antigens on red cells are adsorbed passively from plasma, which must be constantly present for them to be maintained. Three Lewis phenotypes are common amongst Caucasians, namely Le(a^+b^-), Le(a^-b^+), and Le(a^-b^-); the very rare Le(a^+b^+) is detected in Polynesians and Orientals. The carbohydrate structures providing Le^a and Le^b specificity are shown below; these partial structures are linked through other carbohydrate moieties to a **ceramide**, thus forming a glycosphingolipid, or to a protein, thus forming a glycoprotein.

Le^a Gal(β1-3)[Fuc(α1-4)]GlcNAc(β1-3)Gal...

Le^b Fuc(α1-2)Gal(β1-3)[Fuc(α1-4)]GlcNAc(β1-3)Gal...

The structures of the Le^c, Le^d, Le^x, and Le^y determinants are also known. The Lewis antigens are named after a Mrs H. D. G. Lewis, in whom they were first identified. *See also* **galactoside 3(4)-L-fucosyltransferase**.

Lewis base any chemical species that is able to supply an electron pair and is thus able to react with a **Lewis acid** to form an adduct (i.e. Lewis adduct).

Lewis formula *or* **Lewis structure** a depiction of molecular structure in which the valency electrons are shown as dots so placed that each pair of dots represents two electrons. When placed between two atoms each pair of dots also represents a single covalent bond, whereas dots placed adjacent to only one atom represent the non-bonded outer-shell electrons considered to be associated with that atom alone. (e.g. H:C̈l:). A double bond is represented by two pairs of dots (e.g. Ö:: Ö), and so on. Formal charges are attached to atoms as appropriate.

Lewis transferase *see* **galactoside 3(4)-L-fucosyltransferase**.

lexA a gene in *Escherichia coli* encoding a repressor that regulates the genes induced by **SOS repair**. In the latter, following DNA damage, the *lexA* product, LexA, is hydrolysed by RecA protein (*see* ***recA***), thereby allowing the SOS genes to be activated. *lexA* is itself regulated autogenously. LexA binds to operators as a dimer. Database code LEXA_ECOLI, 202 amino acids (22.33 kDa).

lexicographer one who compiles a dictionary, defined by Samuel Johnson (the first English lexicographer) as 'a harmless drudge'. An alternative definition is from *The Enlarged Devil's Dictionary* by Ambrose Bierce, compiled and edited by Ernest J. Hopkins: 'A pestilent fellow who, under the pretense of recording some particular stage in the development of a language, does what he can to arrest its growth, stiffen its flexibility and mechanize its methods.' *See also* the Preface to this present work.

Leydig cell a type of steroid-secreting, interstitial cell that occurs in large numbers between the seminiferous tubules of the testis. The cells secrete androgens, especially testosterone, and this activity is stimulated by luteinizing hormone, for which the cells have specific receptors. [After Franz von Leydig (1821–1908), German anatomist and zoologist.]

LFA 1 a leukocyte cell-surface glycoprotein involved in the adhesion of leukocytes to target cells and thus in a variety of immune phenomena including leukocyte–endothelial cell interaction, cytotoxic T-cell-mediated killing, and antibody-dependent killing by granulocytes and monocytes. It binds to **ICAM**. LFA 1 is a type I membrane glycoprotein belonging to the LEUCAM family of **integrins**; it is a dimer of the α_L and β_2 subunits. Example from human (alpha precursor): database code ITAL_HUMAN, 1170 amino acids (128.70 kDa).

L form (of a bacterium) a defective bacterial cell, of indefinite or spherical shape, in which the cell wall is defective or absent. L forms may develop spontaneously or in response to a variety of stimuli, e.g. thermal or osmotic shock, or the presence of antibiotics that inhibit cell-wall synthesis. They may revert to their original condition on removal of the stimulus or they may reproduce as L forms. On solid media, L forms have a characteristic colonial appearance resembling that of **mycoplasmas** (with which they were originally confused).

lg *symbol for* decadic, or common or Briggsian, **logarithms** (alternative to $\log_{10}$).

LH *abbr. for* luteinizing hormone.

LHC *abbr. for* light-harvesting complex.

LHCP *abbr. for* light-harvesting chlorophyll protein.

LH/FSH-RF *abbr. for* luteinizing hormone/follicle-stimulating hormone releasing factor (i.e. **gonadotropin releasing hormone**).

LHRF *or* **LH-RF** *abbr. for* luteinizing hormone releasing factor (*see* **gonadotropin-releasing hormone**).

LHRH *or* **LH-RH** *abbr. for* luteinizing hormone releasing hormone (*see* **gonadotropin releasing hormone**).

Li *symbol for* lithium.

Libby, Willard Frank (1908–80), US chemist; Nobel Laureate in Chemistry (1960) for 'his method to use carbon 14 for age determination in archaeology, geology, geophysics, and other branches of science'.

+liberin *word ending* denoting a hypothalamic factor (or hormone) that promotes the release (and perhaps also the biosynthesis) of the particular pituitary hormone indicated; e.g. luliberin, thyroliberin. *Compare* **+statin**.

library of genes *see* **gene library**.

librate to oscillate about an equilibrium position. —**libration** *n.*

Librium *see* **chlordiazepoxide**.

licorice *see* **glycyrrhiza**.

Liebermann–Burchard reaction the reaction of acetic anhydride in chloroform with unsaturated steroids (e.g. cholesterol) or triterpenes in the presence of concentrated sulfuric acid to produce a blue-green colour. It is used especially in the estimation of cholesterol.

LIF *abbr. for* leukemia inhibitory factor.

life cycle the totality of functional and morphological stages through which any organism passes between any one developmental stage and the identical stage in the next generation. Less commonly it refers to the totality of the various stages through which an individual organism passes between birth and death.

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Lig *symbol for* the lignoceroyl group, CH_3–$[CH_2]_{22}$–CO–.

ligancy *a less common alternative name for* **coordination number**.

ligand **1** (in a simple inorganic compound) any individual atom, group, or molecule that is attached covalently to the characteristic or central atom or moiety. **2** (in an organic compound) any individual atom or chemical group that is attached covalently to a specified carbon atom; *see also* **point ligand**. **3** (in a coordination entity) **a** any individual atom, ion, or molecule that is attached coordinately to one central metal atom (**unidentate ligand**). **b** an ion, molecule, or molecular grouping that has more than one coordinating group (**bi-**, **tri-**, or **multidentate ligand**). *In both cases the ligand is an electron donor in* the formation of one or more coordinate bonds. **4** an ion of either sign that can associate reversibly with one or more (charged or uncharged) atoms or characteristic molecular groupings in another (usually larger) molecule (as in the hydronation of a conjugate base, the coordination of a metal cation by a protein, etc.). **5** a molecule (or a class of molecules) that has become linked covalently to another molecule to form a conjugate, whether in a single-step reaction or by stepwise addition of its components (e.g. an oligosaccharide moiety in a glycoprotein). **6** a molecule (or part of one) that is bound or is able to bind selectively and stoichiometrically, whether covalently or not, to one or more specific sites on another molecule (as in the combination of antigen with antibody, of hormone with receptor, of substrate with enzyme, etc.). [German: bound element or group, from Latin *ligandus*, gerundive of *ligare* to bind.]

liganded bound by or as a ligand or ligands; ligated; *see* **ligate** (def. 2).

ligand exchange (chromatography) a column-chromatographic technique in which a cation-exchange resin is loaded with a complexable metal ion and the resulting loaded resin, which retains the capability of the metal ion to coordinate to an appropriate complexing agent or ligand, is used for the sorption of that ligand from a solution or a gas phase. Elution is then effected by displacement with, i.e. exchange for, another ligand. The resin is commonly a chelating resin (e.g. a styrene–divinylbenzene copolymer to which iminodiacetate groups are attached) and the ion is usually of a transition metal (e.g. copper or nickel), such ions tending to be bound strongly to these resins. Separation of components of mixtures occurs by virtue of the differences in the stabilities of the various metal–ligand complexes formed.

ligand-field theory *(in inorganic chemistry)* a theory, closely related to the valence-bond theory, that deals with the effects of ligands on the energy levels of the central atom or ion in complexes and crystals. It is especially useful in interpretation of the spectra of inorganic complexes.

ligand-gated describing an ion channel in a cell membrane that is caused to open by the action of an agonist binding to the receptor that governs the channel. Channel opening can be direct, when the receptor acts as an ionophore, or indirect, involving a second messenger regulated by a G-protein.

ligandin *a name formerly given to* a basic dimeric protein of ≈25 kDa per dimeric subunit (*see* **gluthathione transferase**). It is abundant in rat and human liver, kidney, and small intestine. It binds with high affinity to heme, bilirubin, and other organic anions, polycyclic aromatic carcinogens, and various metabolites. In addition it catalyses the conjugation of glutathione with a variety of electrophilic substrates, shows selenium-independent glutathione-peroxidase activity and steroid isomerase activity, and covalently binds activated metabolites of several carcinogens. Ligandin corresponds to the α class of glutathione transferase. Ligandin is present in the pars recta of the proximal renal tubules but does not normally pass into the urine: its presence in the urine, **ligandinuria,** has been used to follow the evolution of various forms of kidney injury, while its presence in serum provides a sensitive indicator in liver injury. Also variously called Y protein, organic anion binding protein, basic azo-dye binding protein, cortisol metabolite binding protein (binder protein I), glutathione-transferase B.

liganding binding by or as a ligand or ligands; ligating; *see* **ligate** (def. 2).

ligandinuria *see* **ligandin**.

ligand-mediated chromatography *a variant of* **affinity chromatography** that employs an additional component, the affinity ligand, which is a ligand both for the reactive component attached to the insoluble matrix and for the substance to be purified. Because the ligand may readily be renewed after completion of each separation, the method is particularly useful when the substance used as the ligand easily becomes degraded or inactivated during the course of a purification.

ligand–receptor assay a form of **saturation analysis** for a hormone or other agonist wherein the specific binding agent used is an isolated preparation of the naturally occurring cellular receptor substance for the agonist. An advantage of the assay is that the values obtained are considered to be a direct reflection of the biological properties of the substance assayed.

ligase **1** *or (formerly)* **synthetase** *the systematic class name for* enzymes of class EC 6, all of which catalyse the ligation of molecules of two substances with concomitant breaking of a diphosphate linkage in a nucleoside triphosphate. The recommended names of particular ligases are formed in some instances, especially those of enzymes of subclass EC 6.4, by using the generic name carboxylase, e.g. pyruvate carboxylase, EC 6.4.1.1. In the remaining instances the generic names ligase (def. 2) or synthase are used, according to whether the name of an individual enzyme is to be based on the names of the reactants or on the name of the product, respectively. **2** *a generic name for* many enzymes of class EC 6 (*see* **ligase** (def. 1)); when added to the names of the two reactants whose ligation is catalysed by a particular enzyme it forms the recommended name of that enzyme; e.g. tyrosine–tRNA ligase (EC 6.1.1.1), acetate–CoA ligase (EC 6.2.1.1). *See also* **synthetase** (def. 2). **3** *see* **DNA ligase**.

ligate **1** to join together, especially with a ligature. **2** *(in chemistry)* to join (molecules or molecular fragments) together with a bond; to coordinate. **3** to bind as or to a **ligand** or ligands. **4** *(in surgery)* to tie off (a blood vessel or duct) with a ligature so as to occlude. —**ligation** *n.*; **ligatable** *adj.*; **ligative** *adj.*

ligatin a filamentous plasma membrane protein for the attachment of peripheral glycoproteins to the external cell surface. It acts as a trafficking receptor for phosphoglycoproteins, localizing them, after internalization, within endosomes. Example (fragment) from human: database code LIGA_HUMAN, 75 amino acids (8.47 kDa).

light **1** electromagnetic radiation capable of producing a visual sensation in the eye. It comprises wavelengths in the range 380–780 nm (frequencies 385–789 THz), although the term is sometimes loosely extended to include some ultraviolet and infrared radiation in adjacent parts of the spectrum. **2** *(in chemistry)* describing any (especially metallic) element whose density is relatively small (usually <5000 kg m^{-3}). **3** *(in physics)* of less than the usual mass. *Compare* **heavy**.

light band a region of a muscle **sarcomere** that stains less densely in light microscopy and low-magnification electron microscopy relative to the **dark bands**; together, these differentially staining bands give the striated appearance of skeletal muscle. The light bands are relatively isotropic in polarized light; they represent the regions occupied by **thin filaments**. *See also* **thick filament**, **Z line**.

light chain **1** *or* **L chain** *or (formerly)* **B chain** *symbol*: L; the shorter of the two main types of polypeptide chain of an **immunoglobulin** of any class. Of ≈22 kDa (human), each light chain is linked at its C-terminal cysteine residue by a disulfide bond to the constant region of a **heavy chain**. In any given animal species, light chains may be distinguished serologically into two types, κ and λ, which occur in immunoglobulin molecules of every class in proportions that vary only with the

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species (about 65% κ in the human), and which have different but homologous sequences. The C-terminal half of each type of light chain consists of a **constant region** and the N-terminal half is a **variable region** possibly related to the antibody-combining site. *See also* **Bence-Jones protein**. **2** any of the four 15–27 kDa polypeptide chains that, with two heavy chains of ≈200 kDa, constitute a molecule of **myosin**.

light-effect mediator *abbr.*: LEM; any of a number of substances that, following their light-induced reduction, activate some of the enzymes of the Calvin cycle (*see* **reductive pentose phosphate cycle**) in photosynthesis. Not all of these mediators have been identified, but it is thought that they are cyst(e)ine-containing proteins that become oxidized in the dark and reduced again in the light. An important member of the group is **thioredoxin**.

light-emitting diode *abbr.*: LED; a device consisting of a semiconductor diode (made, e.g., of gallium arsenide) in which light is emitted at a p–n junction when electrons and holes recombine in a manner proportional to the bias current. It is used to give a visual display of numbers, etc. in calculators, counters, and other pieces of apparatus.

light guide a device consisting of one or more cylinders or strips of transparent material along which light can be made to travel, by means of total internal reflection, in a desired direction and with little loss.

light-harvesting chlorophyll protein *or* **light-harvesting chlorophyll-binding protein** *abbr.*: LHCP; a chlorophyll-binding protein that is abundant in green plants, particularly in those grown at low light intensities. It consists of a 25 kDa polypeptide, encoded by a nuclear gene and synthesized in the cytoplasm, to which is bound most of the chlorophyll *b* and xanthophylls together with some of the chlorophyll *a*. It appears to be capable of transferring the energy of absorbed light photons to both photosystem I and photosystem II. Example, *Lycopersicon esculentum* (tomato) chlorophyll *a-b* binding protein of light-harvesting complex I (type I precursor): database code CB11_LYCES, 246 amino acids (26.57 kDa); residues 1–44 are a transit peptide, 45–246 LHCP. *See also* **light-harvesting complex**.

light-harvesting complex *abbr.*: LHC; a **thylakoid** membrane complex of chorophylls *a* and *b* together with chlorophyll *a-b* binding proteins. In addition, LHCs contain a number of other proteins, the function of which is speculative, together with accessory pigments. The LHCs capture and transfer energy to photosystems I and II. Example, chlorophyll *a-b* binding protein of pea: database code CB21_PEA, 228 amino acids (24.30 kDa). It is regulated by phosphorylation on threonine residues. *See also* **light-harvesting chlorophyll protein**.

light meromyosin *abbr.*: L meromyosin *or* LMM; the smaller, 120 kDa, fragment, also called F3 fragment, produced when **myosin** is subjected to a brief treatment with trypsin or certain other peptidases. It contains much of the helical, rod-shaped tail (>90% α helical) and forms large ordered aggregates at low ionic strength. Light meromyosin has no ATPase activity and cannot bind actin.

light path **1** the path followed by a beam of light when passing through an optical device or a particular part of one. **2** *or* **path length** the length of such a path.

light pen an input/output device for use with a computer that, when pointed at a spot on a visual display unit, can sense whether or not the spot is illuminated; the output current from the light pen can then be used to control the operations of the computer.

light reactions of photosynthesis *or* **light phase of photosynthesis** those reactions of **photosynthesis** in higher plants and algae in which light energy is used to generate NADPH and ATP.

light repair *an alternative name for* **photoreactivation**.

light-scattering a technique used for the determination of the relative molecular mass, M_r, in solution of a macromolecule whose size is large relative to the wavelength of the light used. The value of M_r of the macromolecule can be calculated from the wavelength of the incident light, the angle and intensity of the scattered light, the refractive indices of the solvent and solute, and the concentration of the solute. *See also* **Rayleigh scattering**.

light strand *or* **L strand** **1** a polynucleotide strand not labelled with heavy isotope. **2** the strand in a naturally occurring polynucleotide duplex that is of a lower density than its complementary strand. *Compare* **heavy strand**.

light trapping **1** the process of capturing the energy of incident light in a photosynthetic pigment system. **2** the act or process of using focused light in a liquid medium so arranged as to trap phototactic organisms in a restricted part of that medium.

lignan any member of a class of phenylpropanoid dimers in which the phenylpropane units are linked tail-to-tail and thus having a 2,3-dibenzylbutane skeleton (*compare* **neolignan**). Until recently such compounds had been found only in higher plants, but certain types have now been identified in humans and other mammals as products of the action of gut flora on dietary lignans of plant origin. Guaiaretic acid is structurally one of the simplest; **podophyllotoxin** and more particularly its semisynthetic derivatives **Etoposide** and **Teniposide** have defined actions in clinical medicine, with antitumour and possibly antiviral actions. *See also* **lignin**.

lignify to make or become woody; to accumulate or deposit lignin in the cell walls (of plant tissues). —**lignification** *n.*

lignin any random phenylpropanoid polymer formed in higher plants by the dehydrogenative radical polymerization of various 4-hydroxycinnamyl alcohols, in which the residues are joined in differing proportions and by several different linkages, some of which are nonhydrolysable. Lignin is of high molecular mass, is insoluble in water, and is found in the cell walls of vascular plants (especially of the supporting and conducting tissues), on which it confers strength, rigidity, and resistance to degradation. It is one of the most abundant biopolymers. *See also* **lignan**.

ligninase an enzyme that catalyses breakdown of lignin; strictly most lignin-degrading systems rely on peroxide formed from **oxygenases** to cleave carbon–carbon bonds. An example is diarylpropane peroxidase, EC 1.11.1.14; *systematic name*: diarylpropane:oxygen,hydrogen peroxide oxidoreductase (C–C-bond-cleaving); *other name*: ligninase I. It is a hemoprotein enzyme that catalyses a reaction between 1,2-bis(3,4-dimethoxyphenyl)propane-1,3-diol and H_2O_2 to form 3,4-dimethoxybenzaldehyde, 1-(3,4-dimethylphenyl)ethane-1,2-diol, and $4H_2O$. Example from *Phanerochaete chrysosporium*: database code LIG2_PHACH, 371 amino acids (39.33 kDa).

lignocellulose a covalent adduct of **lignin** and **cellulose**, found in the walls of xylem cells in woody tissues of plants. —**lignocellulosic** *adj.*, *n.*

lignocerate **1** *the trivial name for* tetracosanoate, CH_3–$[CH_2]_{22}$–COO^-, the anion derived from lignoceric acid (i.e. tetracosanoic acid), a saturated straight-chain higher fatty acid. **2** any mixture of lignoceric acid and its anion. **3** any salt or ester of lignoceric acid.

lignoceroyl *symbol*: Lig; *the trivial name for* tetracosanoyl, CH_3–$[CH_2]_{22}$–CO–, the acyl group derived from lignoceric acid (i.e. tetracosanoic acid). It occurs naturally as acylglycerols in peanut and rapeseed oils, and in certain sphingomyelins.

lignoceroyl-CoA synthase *see* **long-chain-fatty-acid–CoA ligase**.

limit *(in mathematics)* a value to which a function or the sum of a series approaches as an independent variable approaches a specified value or infinity.

limit dextrin the highly branched core that remains after exhaustive treatment of amylopectin or glycogen with α- and/or β-amylases. It is formed because these enzymes cannot hydrolyse the (1→6) glycosidic linkages present.

limit dextrinase *see* **α-dextrin endo-1,6-α-glucosidase**, **oligo-1,6-glucosidase**.

limit dextrinosis *an alternative name for* type III **glycogen disease**.

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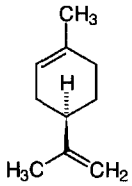
limit digest a digest in which no further degradation can occur under the particular conditions adopted.

limiting current *(in polarography)* the maximal value of the current reached in circumstances when the steady-state current/potential characteristic has a positive slope.

limiting rate *symbol*: *V*; *the recommended name for* the extrapolated rate of an enzyme-catalysed reaction when the enzyme is saturated with substrate(s). It is equal to the product of the stoichiometric concentration of active centres, $[E]_0$, and the catalytic constant, k_0. It can be determined by a number of methods, including graphical methods such as the **Lineweaver–Burk plot**. *Other names*: maximum rate; maximal rate; maximum velocity; maximal velocity.

limiting viscosity number *the recommended name for* **intrinsic viscosity**.

limonene *p*-mentha-1,8-diene; a compound that occurs in many essential oils (e.g. oils of lemon, orange, and dill); both enantiomers and the racemic mixture (i.e. dipentene) occur naturally.



(*R*)-(+) form

LIMS *abbr. for* laboratory information management systems; normally, systems involving automatic electronic data capture and computerized manipulation of data.

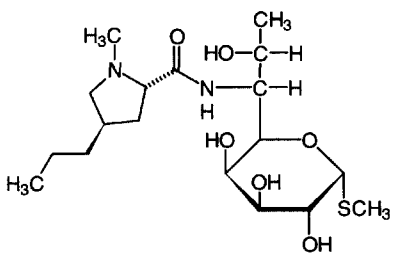
Lin *symbol for* the linoleoyl group, CH_3–$[CH_2]_3$–$[CH_2CH{=}CH]_2$–$[CH_2]_7$–CO– (*all-Z* isomer).

lin3 a gene in *Caenorhabditis elegans* that encodes an **epidermal growth factor**-like type I membrane protein. The protein has two versions (produced by alternative splicing), and is essential for vulval development. Database code LIN3_CAEEL, 438 amino acids (48.87 kDa). *See also* ***let23***.

lin14 a gene involved in embryonic development in *Caenorhabditis elegans* that codes for a nuclear protein. Regulatory sequences in the 3′ untranslated region generate a temporal switch during development. There are three forms of the product: A, database code B40581, 537 amino acids (59.09 kDa); B1, database code A40581, 539 amino acids (59.28 kDa); B2, database code C40581, 515 amino acids (56.65 kDa).

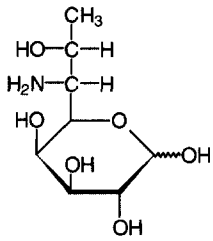
linalool 3,7-dimethyl-1,6-octadien-3-ol; a compound that occurs in linaloe oil and other essential oils; both enantiomers occur naturally. It is used in perfumery.

lincomycin an antibiotic produced by *Streptomyces lincolnensis*. It consists of an amide formed between a substituted pyrrolidine-2-carboxylic acid and methyl 1-thio-α-lincosamine. Lincomycin is active mainly against Gram-positive bacteria; it inhibits protein synthesis by interacting with the 50S ribosomal subunit, inhibiting the early steps of peptide bond formation prior to the formation of polysomes.



lincosamides *generic name for* a group of antibiotics structurally related to **lincomycin**.

lincosamine 6-amino-6,8-dideoxy-D-*erythro*-D-*galacto*-octose; the carbohydrate component of **lincomycin**.



line **1** *(in spectroscopy)* a very narrow band of frequencies of electromagnetic radiation that is noticeably more intense or less intense than adjacent parts of the spectrum; the image of such a line in a spectrogram. **2** *(in biology)* several generations of a family. *See also* **cell line**, **lineage**. —**lineal** *or* **linear** *adj.*

LINE *abbr. for* long interspersed nucleotide element (or sequence or repeat); part of the moderately repetitive DNA of mammalian genomes. Any highly repeated DNA sequence interspersed in a mammalian genome and characteristically several kilobases in length. LINEs are **retroposons** resulting from the action of RNA polymerase II (*see* **RNA polymerase**). Mammalian genomes may contain up to 50 000 copies of particular LINEs. They are regarded as processed **pseudogenes**. The function of LINEs is unknown. *Compare* **SINE**. *See also* **Alu sequence**.

lineage lineal descent, especially from a common ancestor.

linear accelerator a device for producing high-energy particles, in which charged particles are accelerated in a straight line along a long evacuated tube by potential differences applied to a series of circular electrodes along the tube.

linear chain a chain of atoms in a molecule, or a chain of residues in a macromolecule, that is neither branched nor covalently closed.

linear correlation any relationship between two variables such that a graphical plot of one variable against the other is a straight line.

linear density gradient a gradient of linearly and continuously increasing density.

linear dichroism the **dichroism** (def. 1) occurring when linearly polarized light is absorbed by a sample containing partially or completely oriented anisotropic molecules.

linear equation any equation containing any number of variables that is of the first degree, i.e. one in which the variables are all raised to the power of one.

linear growth the growth of a culture such that the number of cells (or the cell mass) increases in direct proportion to the duration of growth.

linearity the condition of being in a straight line.

linearize *or* **linearise** **1** to make linear, i.e. into a straight line. **2** to convert a branched or cyclic form of a (macro)molecule to a linear form, i.e. one with only two ends. —**linearization** *or* **linearisation** *n.*

linearly polarized *or* **plane-polarized** describing light (or other electromagnetic radiation) in which the electric vectors of the vibrations all lie in a given plane containing the light beam. *See* ***polarized light***.

linear velocity the distance moved in a straight line in unit time.

line formula a two-dimensional representation of a molecular entity in which atomic symbols are joined by lines representing single bonds, without any indication or implication of stereochemistry.

line immunoelectrophoresis a one-dimensional single **electroimmunodiffusion** technique, useful for the qualitative and

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quantitative comparison of the antibody spectra of different polyvalent antisera. Samples of antigens to be compared are moulded into adjoining rectangular sample gels along one edge of a gel containing a mixture of the corresponding antibodies, into which the antigens are forced at right angles by electrophoresis. Precipitation lines form parallel to the origin at a distance of antigen migration proportional to the antigen/antibody ratio. Precipitation lines from the samples against the same antibody are continuous and can be directly compared.

line spectrum any spectrum consisting of discrete spectral lines.

Lineweaver–Burk plot a method of plotting enzyme kinetic data. The Michaelis equation is rearranged to give:

$$1/v = K_m/V[S] + 1/V,$$

where K_m is the Michaelis constant, [S] the concentration of the substrate S, v the (initial) rate of reaction at a given value of [S], and V the limiting rate of reaction at infinite [S]. If the Michaelis equation holds for the system, a plot of $1/v$ against $1/[S]$ gives a straight line of slope K_m/V, with intercepts on the $1/v$ axis at $1/V$ and on the $1/[S]$ axis at $-1/K_m$. *See* **Michaelis kinetics**. [After Hans Lineweaver and Dean Burk.]

linewidth the width of a spectral line, usually taken as the distance, in terms of wavelength, frequency, or magnetic flux difference, between the two points of half-peak intensity (half-maximum height).

link *(in chemistry) an informal term for* **bond** (def. 1). *See also* **linkage** (def. 2).

linkage **1** *(in genetics)* an association of two or more non-allelic genes so that they do not show independent **assortment**; i.e. they tend to be transmitted together usually due to physical association on the same chromosome. **2** *(in chemistry) an informal term for* **bond** (def. 1). *See also* **link**.

linkage disequilibrium the preferential association of linked genes/DNA markers in a population; i.e. the tendency for some alleles at a locus to be associated with certain alleles at another locus on the same chromosome with frequencies greater than would be expected by chance alone.

linkage group any group of genes whose members show a marked tendency to segregate as a unit. *See also* **genophore**.

linkage map a map of a chromosome showing in linear order the relative positions of the known genes on that chromosome.

linked genes genes that exhibit **linkage** (def. 1).

linker **1** any small synthetic single-chain oligodeoxynucleotide that is six or more residues long and has a self-complementary base sequence. When self-annealed it forms a stable duplex with blunt ends and containing a **restriction site**. Such linkers are useful for gene splicing. **2** *see* **cross-link**.

linker DNA *see* **chromatin, nucleosome**

linking number *symbol*: L; a topological property of closed circular duplex DNA, defined as the number of turns one strand makes about the other. It must be an integer, and is positive if the turns are right-handed and negative if they are left-handed. It can change only when one or both strands are nicked. It comprises the sum of the **writhing number** (W) and the **twist number** (T), so that a change (ΔL) in the linking number (L) is equal to $\Delta W + \Delta T$.

linoleate **1** *the trivial name for* (*all-Z*)-octadeca-9,12-dienoate, $CH_3–[CH_2]_3–[CH_2–CH=CH]_2–[CH_2]_7–COO^-$, (*all-Z* isomer) the anion derived from linoleic acid, (*all-Z*)-octadeca-9,12-dienoic acid, a diunsaturated straight-chain higher fatty acid essential in the diet of mammals. It occurs naturally as acylglycerols in many vegetable oils and in the lipids of many animal tissues. **2** any mixture of free linoleic acid and its anion. **3** any salt or ester of linoleic acid. *See also* **linoleic family**.

linoleate synthase *see* **phosphatidylcholine desaturase**.

linoleic family (of polyunsaturated fatty acids) a series of polyenoic acids occurring in mammals, in which the hydrocarbon chain terminates with the alkenyl grouping, $CH_3–[CH_2]_4–CH=CH–$ (as in linoleic acid; *see* **linoleate**) and that are synthesized from linoleic acid by chain elongation and/or further desaturation (but which in mammals cannot be synthesized from the corresponding saturated acids or from (9,12,15)-linolenic, oleic, or palmitoleic acids – the latter represent three other series of polyenoic acids). The linoleic family is also known as the ω6, or *n*-6, family because of the position of the double bond nearest the terminal methyl group. The series includes (6,9,12)-linolenic acid, eicosa-11,14-dienoic acid, eicosa-5,11,14-trienoic acid, eicosa-8,11,14-trienoic acid, and arachidonic acid.

linolenate **1** *or* **(9,12,15)-linolenate** *or (formerly)* **α-linolenate** *the alternative trivial names for* (*all-Z*)-octadeca-9,12,15-trienoate; $CH_3–[CH_2–CH=CH]_3–[CH_2]_7–COO^-$ (*all-Z* isomer); the anion derived from (9,12,15)-linolenic acid, (*all-Z*)-octadeca-9,12,15-trienoic acid, a triunsaturated straight-chain higher fatty acid synthesized by plants (notably found in linseed oil) but essential in the diet of mammals (*see* **linolenic family**). The name equally refers to any mixture of (*all-Z*)-octadeca-9,12,15-trienoic acid and its anion, or any salt or ester of this acid. **2 (6,9,12)-linolenate** *or (formerly)* **γ-linolenate** *the trivial name for* (*all-Z*)-octadeca-6,9,12-trienoate; $CH_3–[CH_2]_3–[CH_2–CH=CH]_3–[CH_2]_4–COO^-$ (*all-Z* isomer), the anion derived from (6,9,12)-linolenic acid (*all-Z*)-octadeca-6,9,12-trienoic acid, a triunsaturated straight-chain higher fatty acid belonging to the **linoleic family**. It occurs naturally as acylglycerols in certain plant-seed oils, especially that of the evening primrose (*Oenothera* spp.), and also in small amounts in the lipids of many animal tissues, especially human breast milk. It is the biosynthetic precursor of arachidonate and the prostaglandins. The name refers equally to any mixture of (all-*Z*)-octadeca-6,9,12-trienoic acid and its anion or any salt or ester of the acid.

linolenic family (of polyunsaturated fatty acids) a series of polyenoic acids occurring in mammals, in which the hydrocarbon chain terminates with the alkenyl grouping $CH_3–CH_2–CH=CH–$ (as in (9,12,15)-linolenic acid; *see* **linolenate**). The linolenic family is also known as the ω3 or *n*-3 family because of the position of the terminal double bond three carbon atoms from the methyl end. The longer-chain members of the family can be synthesized in mammals only from dietary (9,12,15)-linolenic acid by chain elongation and/or further desaturation (but not from the corresponding saturated acids or from linoleic, oleic, or palmitoleic acids – the latter represent the other three series of polyenoic acids). If animals are deprived of a source of these fatty acids in the diet, certain tissues, such as the eye, retain existing stores of these fatty acids tenaciously, even in offspring of such animals when the restricted diet is continued for more than one generation. Under these conditions, long-chain acids of the **linoleic family**, e.g. (4,7,10,13,16,)-docosapentaenoic (C22:5 *n*-6) acid, are synthesized in appreciable amounts and presumably partially support the function supplied by long-chain ω3 acids, though the nature of this is unknown. The series includes eicosapentaenoic (C20:5 ω3) and docosahexaenoic (C22:6 ω3) acids, which are found in high concentration in fish oils; these ω3 acids may have value in protecting against heart disease, a role that, if real, would be unrelated to their function as essential fatty acids, since the amount considered necessary for this purpose greatly exceed those needed to fulfil their role as essential fatty acids.

linolenoyl **1** *or* **(9,12,15)-linolenoyl** *or (formerly)* **α-linolenoyl** *symbol*: αLnn *or (sometimes)* Lnn; *the alternative trivial names for* (*all-Z*)-octadeca-9,12,15-trienoyl; $CH_3–[CH_2–CH=CH]_3–[CH_2]_7–CO–$ (*all-Z* isomer); the acyl group derived from (*all-Z*)-octadeca-9,12,15-trienoic acid. **2 (6,9,12)-linolenoyl** *or (formerly)* γ-linolenoyl *symbol*: γLnn; *the trivial names for* (*all-Z*)-octadeca-6,9,12-trienoyl; $CH_3–[CH_2]_3–[CH_2–CH=CH]_3–[CH_2]_4–CO–$ (*all-Z* isomer); the acyl group derived from (*all-Z*)-octadeca-6,9,12-trienoic acid. *See* **linolenate**.

linoleoyl *symbol*: Lin; *the trivial name for* (*all-Z*)-octadeca-9,12-dienoyl; $CH_3–[CH_2]_3–[CH_2–CH=CH]_2–[CH_2]_7–CO–$ (*all-Z* isomer); the acyl group derived from linoleic acid. *See* **linoleate**.

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liothyronine *a pharmaceutical name for* L-3,5,3′-**triiodothyronine**.

lip+ *a variant form of* **lipo+** (before a vowel).

lipaemia *a variant spelling (esp. Brit.) of* **lipemia**.

lipase **1** *(in enzyme nomenclature) a general term for* any acylglycerol carboxylic ester hydrolase, of EC sub-subclass 3.1.1. The term may be incorporated in the enzyme name as the suffix '+lipase'. **2** *abbr. (in clinical chemistry)*: LPS; *an alternative name for* **triacylglycerol lipase**. *See also* **hormone-sensitive lipase**, **lipoprotein lipase**, **pancreatic lipase**.

lipemia *or* **lipidemia** the condition when there is a greater than normal content of lipid in the blood, e.g. after a fatty meal or in certain pathological states. *Also (esp. Brit.)* **lipaemia**, **lipidaemia**.

lipid *or (formerly)* **lipide** *or* **lipoid** *or* **lipin(e)** **1** any member of a large and diverse group of oils, fats, and fatlike substances that occur in living organisms and that characteristically are soluble in **lipid solvents** but only sparingly soluble in aqueous solvents. Lipids constitute one of the four major classes of compounds found in living tissues (the others being carbohydrates, proteins, and nucleic acids) and they include: (1) fatty acids; (2) neutral fats (i.e. triacylglycerols), other fatty-acid esters, and soaps; (3) long-chain (or fatty) alcohols and waxes; (4) sphingoids and other long-chain bases; (5) glycolipids, phospholipids, and sphingolipids; and (6) carotenes, polyprenols, sterols (and related compounds), terpenes, and other isoprenoids. See individual entries for details. **2** any oily, fatty, or fatlike material that occurs in living organisms. **3** of, concerned with, for, or relating to **lipid** (def. 2); consisting of or containing **lipid** (def. 1, 2); **lipoid** (def. 1) or lipoidal. —**lipidic** *adj.*

lipid A the glycolipid moiety of bacterial **lipopolysaccharide**.

lipidaemia *a variant spelling (esp. Brit.) of* lipidemia; *see* **lipemia**.

lipid bilayer any layer, two molecules thick, of amphipathic lipid molecules. If it is surrounded by a polar environment, the polar parts of the lipid molecules are oriented outwards towards the environment and the nonpolar parts inwards into the interior of the bilayer. The two layers of lipid are referred to as **leaflets**, e.g. the inner and outer leaflets of the bilayer. *See also* **black lipid membrane**.

lipide *a variant spelling of* **lipid**.

lipidemia *an alternative term for* **lipemia**.

lipidosis *or* **lipoidosis** (*pl.* **lipidoses** *or* **lipoidoses**) any clinical disorder, *also called* **lipid storage disease**, that results in the excessive deposition within specific tissues of particular types of lipids. Many lipidoses are inherited disorders of galactosphingolipid metabolism.

lipid-soluble *a vague term applied to* various classes of nonpolar substances, e.g. sterols, certain vitamins, carotenoids, and polyprenoids, that are commonly present in small amounts in association with the major lipid.

lipid solvent any relatively nonpolar solvent that can be used to extract lipids from tissues or other materials.

lipid storage disease *an alternative term for* **lipidosis**.

lipin *or* **lipine** *a former term for* **lipid** (def. 1), especially one containing nitrogen and/or phosphorus.

Lipmann, Fritz Albert (1899–1986), German-born US biochemist; Nobel Laureate in Physiology or Medicine (1953) 'for his discovery of co-enzyme A and its importance for intermediary metabolism' [prize shared with H. A. Krebs].

lipo+ *or (before a vowel)* **lip+** *comb. form* denoting lipid, lipid-containing, or lipid-like.

lipoamide *or (sometimes)* **lipoyllysine** a **lipoyl** group when in amide linkage to the ε-amino group of a specific lysine residue in dihydrolipoamide acetyltransferase (EC 2.3.1.12) and dihydrolipoamide succinyl transferase (EC 2.3.1.61), which form, respectively, parts of the **pyruvate dehydrogenase complex** and the **2-oxoglutarate dehydrogenase complex**.

lipoamide reductase (NADH) EC 1.8.1.4; *recommended name*: dihydrolipoamide dehydrogenase; *other names*: E3 component of α-ketoacid dehydrogenase complexes; lipoyl dehydrogenase; dihydrolipoyl dehydrogenase; diaphorase. An enzyme that catalyses the oxidation by NAD^+ of dihydrolipoamide to form lipoamide and NADH. FAD is a coenzyme. It is typically a homodimer, occurring in the mitochondrial matrix (in eukaryotes), with a redox-active S–S bond similar to glutathione reductase. Example (precursor) from yeast (the first 21 amino acids form the mitochondrial transit peptide): database code DLDH_YEAST, 499 amino acids (53.95 kDa).

lipoate **1** 1,2-dithiolane-3-pentanoate, the anion derived from **lipoic acid** (i.e. thioctic acid). **2** any salt or ester of lipoic acid.

lipocaic a substance extractable from the pancreas that was said to be lipotropic in pancreatectomized animals.

lipocalin any of a large group of ligand-binding proteins, particularly one that binds hydrophobic ligands, e.g. biliverdin pheromone. The family includes retinol-binding protein, α-microglobulin, insect bilin-binding proteins, and **beta lactoglobulin**. The name derives from the fact that the ligand is enclosed by the protein as a flower is enclosed by the calyx (i.e. the sepals). All members of the family have a similar β-barrel structure of eight barrels crossing in the centre; different ligand-binding properties are determined by loops on the periphery. *See also* **Appendix E**.

lipochrome *a former name for* any of various lipid-soluble biological pigments.

lipocortin *see* **annexin**.

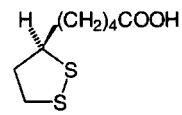
lipofection a lipid-mediated DNA-transfection technique that makes use of unilamellar liposomes that contain a cationic lipid and spontaneously react with DNA.

lipofuscin any of various brownish lipid-soluble pigments that are deposited in animal cells, especially in senility.

lipogenesis the formation of fat. The term is applied especially to the processes by which higher fatty acids are synthesized from nonlipid sources. —**lipogenic** *adj.*

lipogenic amino acid any amino acid that can provide carbon atoms for the biosynthesis of higher fatty acids.

lipoic acid *or* α-lipoic acid *symbol*: $Lip(S_2)$; 1,2-dithiolane-3-pentanoic acid; thioctic acid; the naturally occurring form is the (*R*)-(+)-enantiomer. Lipoic acid provides the reversibly reducible moiety, **lipoyl**, of **lipoamide** and is a growth factor for certain microorganisms. The reduced form is dihydrolipoic acid, $HS–CH_2–CH_2–CH(SH)–[CH_2]_4–COOH$ (*symbol*: $Lip(SH)_2$); the redox potential of the system is –0.29 V at pH7. Lipoic acid is an essential component of the α-ketoacid dehydrogenase complexes. *See* **pyruvate dehydrogenase complex** and **2-oxoglutarate dehydrogenase complex**.



lipoid **1** *or* **lipoidal** being or resembling an oil or a fat; oily, fatty. **2** *a former term for* **lipid** (def. 1, 2).

lipolysis the breakdown of lipids, especially the (enzymic) hydrolysis of acylglycerols. —**lipolytic** *adj.*

lipolytic hormone *an alternative name for* **lipotropin**.

lipomodulin *or* **annexin I** a 40 kDa regulatory protein isolated from rabbit neutrophils that, in its nonphosphorylated form, is an inhibitor of phospholipase A_2 and that on phosphorylation by a cyclic-AMP-dependent protein kinase loses this inhibitory property. It has been suggested that lipomodulin thereby regulates the release of arachidonate from leukocytes, or other cells, that may occur in response to chemoattractants and other external stimuli.

lipophilic tending to dissolve in, having a strong affinity for, or readily mixing with lipids or substances of low polarity. *See also* **hydrophilic**, **lyophilic**. —**lipophilicity** *n.*

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lipophilin *another name for* myelinproteolipid. *See* **myelin protein**.

lipophorin any member of the major class of lipid-transporting proteins found in the hemolymph of insects. In locusts the apoprotein is synthesized in the fat body as an 85 kDa polypeptide. *See also* **apolipophorin**.

lipophosphoglycans *see* **GPI anchor**.

lipopolysaccharide *abbr.*: LPS; any of a group of related, 10 kDa, structurally complex components of the outer leaflet of the outer membrane of Gram-negative bacteria. Lipopolysaccharide molecules consist of three covalently linked regions: lipid A, core oligosaccharide, and an O side chain. The innermost layer, lipid A, which is responsible for the toxicity of the lipopolysaccharide, consists of six fatty acyl chains (sometimes hydroxylated) linked in various ways to two glucosamine residues. The branched core oligosaccharide contains ten saccharide residues, several of them unusual, and has a structure that appears to be similar in closely related bacterial strains. The outermost O side chain, which is highly variable and determines the antigenic specificity of the organism, is made up of many (≈50) repeating units of a branched tetrasaccharide containing further unusual sugar residues.

lipopolysaccharide *N*-acetylglucosaminyltransferase EC 2.4.1.56; an enzyme of the lipopolysaccharide core biosynthetic pathway in enteric bacteria; it catalyses a reaction between UDP-*N*-acetyl-D-glucosamine and lipopolysaccharide to form UDP and *N*-acetyl-D-glucosaminyllipopolysaccharide. Example from *Salmonella typhimurium*: database code RFAK_SALTY, 381 amino acids (43.10 kDa). There is little similarity between the given example and the corresponding enzyme in *Escherichia coli*. *See also* **glycolipid**.

lipoprotein any conjugated, water-soluble protein in which the nonprotein moiety consists of a lipid or lipids. The lipid may be triacylglycerol, cholesterol, or phospholipid, or a combination of these. *Compare* **proteolipid**.

lipoprotein(a) one or two molecules of apolipoprotein(a) linked by a disulfide bridge to **apolipoprotein B**-100; it may be a physiological inhibitor of plasminogen activation. Levels in human plasma (which range from undetectable to 100 mg dL^{-3}) show correlation with the incidence of atherosclerosis.

lipoprotein lipase EC 3.1.1.34; *abbr.*: LPL; *other names*: clearing factor lipase; diglyceride lipase; diacylglycerol lipase. An enzyme that catalyses the hydrolysis of triacylglycerol to diacylglycerol and fatty-acid anion. Its function, after uptake of dietary lipid, is to hydrolyse triacylglycerols in chylomicrons and very-low-density lipoproteins, to diacylglycerols and fatty-acid anions; the fatty acids are then taken into peripheral tissues for futher metabolism; it will also hydrolyse diacylglycerols. It acts in the presence of apolipoprotein C-II on the luminal surface of vascular endothelium. It is a **GPI-anchor** dimer, and is released by heparin, etc. Example (precursor) human: database code LIPL_HUMAN, 475 amino acids (53.10 kDa).

lipoprotein signal peptidase *see* **prenurein-leader peptidase**.

liposome **1** a natural lipid globule suspended in the cytoplasm of some cells. **2** any small, roughly spherical, artificial vesicle consisting of a continuous bilayer or multibilayer of complex lipids enclosing some of the suspending medium. Liposomes are formed by allowing complex lipids to 'swell' in aqueous solution sometimes with the aid of sonication. They are used experimentally as models of biological membranes and therapeutically for entrapment of drugs, enzymes, or other agents with a view to their more effective delivery to target cells. Originally, such a structure was termed a cellule (when bilayered), smectic mesophase, spherule, or spherulite. *See also* **liquid crystal**.

lipotaurine the 7,13-dihydroxy-2-*trans*-octadecenoyl amide of taurine. It is found in the lipid fraction of *Tetrahymena thermophila*.

lipoteichoic acid any of a group of **teichoic acids** that contain lipid, are present in the membranes of all species of Gram-positive bacteria so far examined, and, unlike wall teichoic acids, are extractable with hot water or phenol.

lipotropic *or* **lipotrophic** tending to prevent the accumulation of, or to remove, abnormal amounts of lipid (in a tissue or organ, e.g. adipose tissue, liver).

lipotropic agent *or* **lipotropic substance** any substance capable of preventing or correcting fatty infiltration of the liver caused by choline deficiency.

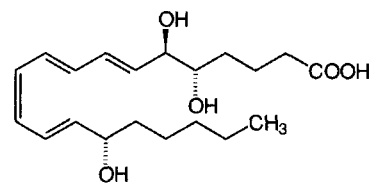
lipotropic hormone *or* **lipotrophic hormone** *a former name for* **lipotropin**.

lipotropin *or* **lipotropic hormone** (*abbr.*: LPH) either of two polypeptides, β- and γ-lipotropin, that can be isolated from the anterior and intermediary lobes of mammalian pituitary glands and are characterized by their ability to elicit lipolysis in adipose tissue. β-Lipotropin corresponds in sequence to the 91 C-terminal amino-acid residues of **proopiomelanocortin**, and γ-lipotropin corresponds to the 58 N-terminal residues of β-lipotropin. In fact, they are of no greater lipotropic potency than corticotropin and α-melanotropin, and whether they have any intrinsic physiological function is still uncertain. Both β- and γ-lipotropins are found in normal human blood. *Other names*: lipolytic hormone; adipokinetic hormone; *former names*: lipotrophin; lipotrophic hormone.

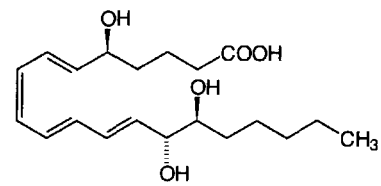
lipotropism the state or quality of being lipotropic.

lipovitellin a ≈135 kDa phospholipoprotein that, together with phosvitin, constitutes the bulk of the yolk proteins of the eggs of oviparous vertebrates. These two proteins are synthesized and secreted by the liver as a single large molecule, **vitellogenin**, which is taken up by the ovary and split into the two components.

lipoxin *abbr.*: LX; any of a group of eicosanoids containing a conjugated tetraene structure and having three hydroxyl groups. They are generated by the action of **lipoxygenase** enzymes on polyunsaturated fatty acids (arachidonate and eicosapentaenoate). The major lipoxins, A_4 and B_4, are derived from arachidonate; lipoxin A_4 (LXA_4) is (7*E*,9*E*,11*Z*,13*E*)-(5*S*,6*R*,15*S*)-5,6,15-trihydroxy-eicosa-7,9,11,13-tetraen-1-oate; lipoxin B_4 (LXB_4) is (6*E*,8*Z*,10*E*,12*E*)-(5*S*,14*R*,15*S*)-5,14,15-trihydroxy-eicosa-6,8,10,12-tetraen-1-oate. LXA_4 has been found to cause contraction of guinea-pig lung strips, but not ileum; LXA_4 and LXB_4 cause dilatation of arterioles.



lipoxin A_4



lipoxin B_4

lipoxygenase **1** EC 1.13.11.12; *systematic name*: linoleate:oxygen 13-oxidoreductase; *other names*: lipoxidase; carotene oxidase. An enzyme that catalyses the oxidation by dioxygen of linoleate to (9*Z*,11*E*)-(13*S*)-13-hydroperoxyoctadeca-9,11-dienoate (*abbr.*: 13(*S*)-HpODE); iron is a cofactor. **2** any member of a group of dioxygenase enzymes that catalyse the oxidation of polyunsaturated fatty acids to a particular corresponding hydroperoxide. Such enzymes are

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widely distributed in plants and in animals from invertebrates to humans. They are found variously in leukocytes, mast cells, platelets, and lung, their positional specificities varying from tissue to tissue; notably a 12-lipoxygenase predominates in platelets, and a 5-lipoxygenase in neutrophils. They are important in the conversion of arachidonate to 5- and 12-hydroperoxyeicosatetraenoates (the 5-hydroperoxy compound being the biosynthetic precursor of the leukotrienes). Lipoxygenase activity has also been observed upon a variety of polyunsaturated fatty acids, indicating that such enzymes exist in a wide variety of forms. The configuration at the oxidized carbon is most often *S*, but *R* products are known, e.g. of sea urchin egg lipoxygenase. Of the three main lipoxygenase activities, the function of 12-lipoxygenase (EC1.13.11.31) remains to be clarified; 5-lipoxygenase (EC 1.13.11.34) is important in yielding precursors for **leukotriene** biosynthesis; 15-lipoxygenase (EC 1.13.11.33) yields precursors for the **lipoxins**. All three, however, are involved in the synthesis of hydroperoxy- and dihydroxy-eicosatetraenoates. Compounds that inhibit both lipoxygenase and prostaglandin-endoperoxide synthase include **curcumin**, **eicosatetraynoic acid**, and phenidone (1-phenyl-3-pyrazolidinone). Compounds that selectively inhibit lipoxygenases without inhibiting prostaglandin-endoperoxide synthase include **eicosatriynoic acid** and **esculetin**. *See also* **dihydroxyeicosatetraenoate, hydroperoxyeicosatetraenoate, hydroperoxyoctadecadienoate, hydroxyeicosatetraenoate**.

lipoyl the acyl group, 1,2-dithiolane-3-pentanoyl, derived from **lipoic acid**. It provides the reversibly reducible moiety of **lipoamide**.

lipoyllysine *an alternative name for* **lipoamide**.

Lip(S_2) *symbol for* a residue of (the oxidized form of) **lipoic acid**.

Lip($SH)_2$ *symbol for* a residue of dihydrolipoic acid, the reduced form of **lipoic acid**.

lipstatin an irreversible inhibitor of several lipases, e.g. pancreatic, gastric, carboxyl ester, or bile-stimulated lipase of milk, isolated from *Streptomyces toxytricini*. It blocks fat absorption selectively.

lipuria the presence of lipid or oily droplets in the urine.

liquefy *or* **liquify** to become, or cause to become, liquid. —**liquefaction** *or* **liquifaction** *n*.

liquid **1** a state of matter, intermediate between a solid and a gas, in which the molecules are relatively free to move with respect to each other but are restricted by intermolecular forces strong enough to prevent spontaneous expansion or significant compression. **2** any substance that is liquid at normal room temperature and pressure. **3** of, pertaining to, being, or behaving as a liquid. *Compare* **fluid**.

liquid air a pale-blue liquid containing principally liquid nitrogen and liquid oxygen, b.p. –194.35 °C (78.80 K), obtained by compressing and cooling gaseous air. It is used as a refrigerant and in the preparation of nitrogen and oxygen.

liquid chromatography *abbr.*: LC; any form of **chromatography** in which a liquid is used as the mobile phase.

liquid crystal *or* **mesomorphic state** *or* **mesophase** any new phase, resembling both liquid and solid phases, that appears when certain pure liquids are cooled, or pure solids are heated. These new phases have a translucent or cloudy appearance. In liquids of asymmetric molecules the molecular axes are arranged at random. In liquid crystals, however, there is some alignment, which occurs in three main distinguishable modes (certain such mesomorphic substances displaying more than one). In **nematic liquid crystals** the long axes of the molecules are aligned parallel to each other but the molecules are not arranged in layers. These scatter light strongly and appear translucent. In **cholesteric liquid crystals** the molecular axes are aligned and the molecules are arranged in layers but the orientation of the axes changes in a regular way on going from one layer to the next. Because the distance between any two layers with the same molecular orientation is of the order of the wavelength of visible light such crystals display vivid iridescence. **Smectic liquid crystals** are formed by certain molecules that have chemically dissimilar parts, e.g. polar and nonpolar; the chemically similar parts attract one another and the molecules form layers and align themselves in one direction. *See also* **liquid-crystalline phase**.

liquid-crystal display *abbr.*: LCD; any display of characters or numbers in a calculator, clock, or other device, based on **liquid crystal** cells whose reflectivity is changed by application of an electric field

liquid-crystalline phase any of several types of phase adopted by polar lipids at moderately elevated temperatures. Two major types exist, the lamellar and hexagonal phases. In the lamellar phase, also known as the L_α phase, the lipids form sheets of bilayers with the polar groups oriented outwards and the fatty-acyl moieties oriented into the hydrophobic core between the two bilayers. Such a phase is likely to include many such bilayers stacked on top of each other, with their polar groups apposed. In the hexagonal phase, the lipids form a spherical aggregate, in which the polar headgroups may be oriented either into the centre of the sphere, when this is known as the H_1 phase, or towards the surface of the sphere, the H_2 phase. In liquid-crystalline phase, the lipid adopts a looser packing, with greater mobility of the fatty-acyl chains than in the crystalline state. At low temperatures, in the absence of water, lipids exist in a crystalline state. If the lipid is heated to a point that attains the **transition temperature**, a temperature characteristic of each pure compound, the lipid undergoes a transition to one of the liquid-crystalline phases. On further heating, it melts completely. Addition of water at low temperature to the crystalline state causes formation of a gel phase, with water layers between the apposed polar headgroups. This gel phase will, on heating to the transition temperature, undergo transition to a liquid-crystalline phase similar to those described above.

liquid-gel chromatography a type of liquid chromatography in which the stationary phase is a gel. It includes **gel-permeation chromatography** and **ion-exchange chromatography**.

liquid glucose *an alternative name for* **corn syrup**.

liquid-junction potential the electric potential, not experimentally measurable, that arises across the boundary of two solutions of different compositions, e.g. between two half-cells. It is a complex function of the activities and transference numbers of the several ions in the transition layer.

liquid–liquid chromatography *abbr.*: LLC; a type of liquid chromatography in which the stationary phase is a liquid supported on a solid.

liquid medium any liquid **culture medium**.

liquid nitrogen nitrogen in the liquid state. It has a b.p. of –195.79 °C (77.36 K), and is useful as a cooling and freezing agent.

liquid oxygen oxygen in the liquid state. It has a b.p. of –182.96 °C (90.19 K).

liquid paraffin a colourless, odourless fraction of higher liquid hydrocarbons obtained from petroleum. Light liquid paraffin has a density of 0.83–0.86 g ML^{-1} and heavy liquid paraffin has a density of 0.86–0.89 g ML^{-1}. It is used for (hot) oil baths, and the purified material is used as a suspending medium in infrared spectroscopy.

liquid-scintillation counting *abbr.*: LSC; a technique for counting particulate radiation. The (radioactive) sample is dissolved or suspended in, or placed in close approximation to, a solvent containing one or more substances that are fluorescent and emit a pulse of light (scintillation) when excited by an incident ionizing particle or photon. The light is detected by photomultipliers, in a liquid-scintillation counter.

liquid-scintillation spectrometry **liquid-scintillation counting** of particulate radiation of one or more selected ranges of energies.

liquid-solid chromatography *abbr.*: LSC; a type of liquid chromatography in which the mobile phase is a liquid and the stationary phase a solid.

liquor **1** *(in pharmacy)* a (usually aqueous) solution of a pure

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substance. **2** a solution in a chemical manufacturing process. **3** the water used in brewing.

liquorice *or (esp. US)* **licorice** *or* **glycyrrhiza** the dried roots and rhizome of *Glycyrrhiza glabra*. This preparation contains glycyrrhizin, the glucoside of glycyrrhetic acid; it resembles **aldosterone** and has effects similar to the **mineralocorticoids**.

LISP a high-level computer language used for artificial intelligence. [Acronym from 'list processing'.]

liter *the US spelling of* **litre**.

lithiasis *(in pathology)* the presence of calculi (stones), e.g. in the biliary or urinary tracts.

lithium *symbol*: Li; an element of group 1 of the IUPAC **periodic table**; atomic number 3; relative atomic mass 6.939. It is a soft, silvery white, alkali metal of such high reactivity that it must be stored in an inert atmosphere or under oil. It is not found free in nature, occurring in the minerals spodumene and lepidolite. Lithium carbonate, Li_2CO_3 (commonly referred to as 'lithium') is used to control the symptoms of manic-depressive illness. Li^+ inhibits inositol phosphate phosphatase, thereby inhibiting the recycling of inositol, and reducing its availability for phosphatidylinositol synthesis.

lithogenesis *(in pathology)* the processes leading to formation of calculi (stones). —**lithogenic** *adj.*

lithotroph any member of either of two groups of organisms, chemoautotrophs (*see* **chemotroph**) and **photolithotrophs**, that use CO_2 as a carbon source.

litre *or (US)* **liter** *symbol*: L *or* l; a non-SI unit of volume, now identical to the cubic decimetre; i.e. 1 L = 1 dm^3 = 10^{-3} m^3.

little gastrin *see* **gastrin**.

liver one of the largest organs of the vertebrate body, situated in the abdominal cavity and formed as a diverticulum of the gut. It is highly vascular; venous blood carrying the products of digestion enters via the hepatic portal vein, while arterial blood enters via the hepatic artery. Blood leaves via the hepatic vein. The liver functions as a gland by secreting **bile** and is an important site of metabolism of carbohydrates, proteins, and fats; it stores carbohydrate as **glycogen**, is active in **gluconeogenesis**, and is important in the regulation of the blood glucose level. It is also an important site for the synthesis of **urea** and **ketone bodies**. The liver synthesizes **fibrinogen**, **prothrombin**, **serum albumin**, and other blood proteins and plays an important part in **detoxication**. The major cells in the liver are the **hepatocytes**. The liver also contains **Kupffer cells** of the reticuloendothelial system, cells derived from the bile duct cannuliculae, and fibroblasts, which are particularly important in the pathogenesis of liver cirrhosis. *See also* **regeneration** (def. 2).

LLC *abbr. for* liquid–liquid chromatography.

LLD factor *abbr. for Lactobacillus lactis* Dorner factor; a growth factor for this organism, identical to **vitamin B_{12}**.

LLF *or* **L-L factor** *abbr. for* Laki–Lorand factor, i.e. factor XIII (*see* **blood coagulation**).

lm *symbol for* **lumen** (def. 1).

L meromyosin *abbr. for* light meromyosin.

LMM *abbr. for* light meromyosin.

ln *symbol for* natural, or Napierian, **logarithm** (alternative to $\log_e$).

αLnn *or (sometimes)* **Lnn** *symbol for* the linolenoyl *or* (9,12,15)-linolenoyl *or (formerly)* α-linolenoyl group; *see* **linolenoyl** (def. 1).

γLnn *symbol for* the (6,9,12)-linolenoyl *or (formerly)* γ-linolenoyl group; *see* **linolenoyl** (def. 2).

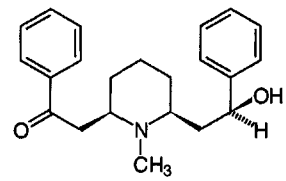
lnRNA *abbr. for* low-molecular-weight nuclear RNA (*see* **small nuclear RNAs**).

load *(in metabolic studies)* the amount (of a specified substance) given in a metabolic test.

loading test *or* **load test** a metabolic test in which the subject is given a dose of a specific substance and the concentration in blood and/or urine of the substance, or of some related metabolite, is determined as a function of time. Such a test is useful for determining the capacity of a particular metabolic pathway in the subject.

lobelia **1** any plant of the genus *Lobelia*. **2** *or* **Indian tobacco** the dried leaves, shoot tips, and seeds of *Lobelia inflata*, which contain the alkaloid **lobeline**.

lobeline 2-[6-(β-hydroxyphenethyl)-1-methyl-2-piperidyl]acetophenone; an alkaloid derived from **lobelia** (def. 2) with actions on the central and peripheral nervous systems that resemble those of **nicotine**. It is responsible for some of the properties of herbal cigarettes.



(–)-lobeline

Lobry de Bruyn–van Ekenstein transformation a non-enzymic transformation occurring in carbohydrates, usually in alkaline conditions, that includes epimerization of both aldoses and ketoses and aldose–ketose isomerization. [After Cornelius Adrian Lobry de Bruyn and W. Alberda van Ekenstein (1857–1937), who first described it in 1895.]

localized melting the (reversible) destabilization of tertiary structure in a limited region of an ordered biopolymer through interaction with a specific agent, e.g. an enzyme.

locant a prefix or infix used in organic chemical nomenclature to identify the position of a substituent in a parent structure or of an isotopic modification to a compound. Locants are commonly Arabic numerals, but Greek letters and italicized symbols of heteroatoms are also used. In isotopically modified compounds the italicized name of the function containing the modification may be used if it has no number, e.g. in [*methyl*-^{14}C]methionine.

loci *the plural of* **locus**.

lock-and-key model a model for the mechanism of an enzyme–substrate combination, of a hormone–receptor interaction, or of an antibody–antigen reaction. In this model, which is based on the analogy of the complementarity of a lock and its key, one reactant is envisaged binding to the other on a site to which it is structurally complementary.

Locke's solution *or* **Locke solution** *or* **Ringer–Locke solution** any one of several balanced salt solutions modified from **Ringer's solution**, initially for the perfusion of mammalian heart and other tissues in physiological experiments. Such solutions have usually contained (in grams per litre, approx.) NaCl (9.0–9.5), KCl (0.20–0.42), $CaCl_2$ (anhydrous, 0.20–0.24), $NaHCO_3$ (0.1–0.3), and glucose (1.0–2.5). [After Frank Spiller Locke (1871–1949), British physiologist, who devised them in 1894 and 1900.]

lock-washer structure a putative intermediate structure formed during the assembly of subunits of the coat protein of tobacco mosaic virus into the helically organized structure of the fully formed virion. It is believed to arise after the primary subassembly, which is a two-layered disk with 17 subunits per layer, has self-aggregated into a cylinder; a dislocation in each disk then occurs so that it becomes a two-turn flattened protohelix, of similar shape to a lock washer of the sprung type.

loco disease *see* **locoweed**.

locoweed any of various plants belonging to the genera *Astragalus* or *Oxytropis*, found mainly in western USA. They contain L-2-amino-3-(methylseleno)propionic acid (methylselenocysteine), a nonprotein amino acid, and may cause poisoning (**loco disease**) when ingested by livestock. [From Spanish *loco*, mad.]

locus (*pl.* **loci**) **1** *(in genetics)* the specific position, in all homologous chromosomes, of a particular gene or one of its alleles. **2** *(in mathematics)* the curve or line traced by a point moving so as to satisfy a particular set of conditions.

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locus control region *abbr.*: LCR; a group of five regions upstream of the structural genes for the β chain of hemoglobin in human and mouse. These regions are essential for the expression of all the genes of the β-like gene cluster.

lod score *abbr. for* log of the odds score; a statistical test to determine whether a set of linkage data indicates linkage or not, the $\log_{10}$ of the odds favouring linkage. For genetic disorders that are not X-linked, a lod score of +3 (1000:1 odds of linkage) indicates linkage, whilst a score of –2 is odds of 100:1 against linkage.

Loewi, Otto (1873–1961), German-born US physiologist; Nobel Laureate in Physiology or Medicine (1936) jointly with H. H. Dale 'for their discoveries relating to chemical transmission of nerve impulses'.

log **1** *symbol for* logarithm. **2** *abbr. for* logarithmic.

logarithm *abbr. and symbol*: log; the power to which a fixed number (the base) must be raised in order to produce a specified number; i.e. in the expression $a = b^n$, a is the specified number, b is the base, and n is the logarithm. In **decadic (common)** or **Briggsian, logarithms** the base is 10; the common logarithm of a is written as $\log_{10}a$, or lg a. In **natural**, or **Napierian, logarithms** the base is e (= 2.718 28...); the natural logarithm of a is written as $\log_e a$ or ln a. In **binary logarithms** the base is 2, and the binary logarithm of a is written as $\log_2 a$ or lb a. In converting between them, $\log_e a = 2.303 \times \log_{10} a$, and $\log_2 a = 3.322 \times \log_{10} a$.

logarithmic *or* **logarithmical** *abbr.*: log; **1** of, pertaining to, using, or containing **logarithms** of numbers or variables. **2** describing a relationship in which one variable is proportional to the logarithm of another.

logarithmic growth a type of growth pattern shown by bacteria or other cells in which the number of cells, or the cell mass, increases logarithmically (exponentially) with time. The rate of increase at any time is proportional to the number of cells, or the cell mass, present.

logarithmic phase *abbr.*: log phase; the phase of growth of bacterial or other cells during which they undergo **logarithmic growth**.

logarithmic plot *abbr.*: log plot; a graph in which one axis has a **logarithmic** (def. 1) scale and the other a linear scale.

logical operation an operation on **binary** numbers or statements used in computing and also in applications such as databases and library searches. There are three common binary operators (AND, OR, XOR) and one **unary operator** (NOT).

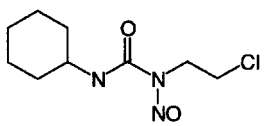
log–log plot double logarithmic plot; a graph on which both variables are plotted logarithmically.

Lohmann reaction *a name sometimes given to* the reversible reaction, catalysed by **creatine kinase**, in which ATP and creatine are formed from ADP and phosphocreatine. [After Karl Lohmann (1898–1978), German biochemist.]

Lohmann's enzyme *an alternative name for* **creatine kinase**.

lombricine the 2-guanidoethanol phosphoester of phosphoserine. In earthworms, the guanidine group can undergo phosphorylation to phospholombricine, which acts as a **phosphagen**.

lomustine 1-(2-chloroethyl)-3-cyclohexyl-1-nitrosourea; a chloroethylnitrosourea derivative with actions resembling **carmustine**.



London forces *see* **dispersion forces**.

lone pair *or* **nonbonding electrons** a pair of electrons of opposite spins occupying the same orbital in the valence shell of an atom.

long-acting thyroid stimulator *abbr.*: LATS; an IgG immunoglobulin found in the serum of a large proportion of thyrotoxic patients. It binds competitively with thyrotropin to thyrotropin receptors in thyroid plasma membrane, stimulates membrane adenylate cyclase, and causes longer-lasting stimulation of thyroid-hormone secretion than thyrotropin itself.

long-chain describing an aliphatic compound of any type with a chain length greater than ten carbon atoms (i.e. C_{10}).

long-chain alcohol *or* **fatty alcohol** any aliphatic compound with a chain length greater than C_{10} that possesses a terminal hydroxymethyl group. They are components of **ether lipids**, and esterified with long-chain fatty acids they form wax esters, often major components of plant cuticular waxes.

long-chain-alcohol *O*-fatty-acyltransferase EC 2.3.1.75; *other name*: wax synthase; an enzyme that catalyses the formation of a long-chain fatty acyl ester, i.e. a wax, from acyl-CoA and a long-chain alcohol with release of CoA.

long-chain base any aliphatic compound with a chain length greater than C_{10} that possesses a terminal basic group.

long-chain fatty acid any aliphatic compound with a chain length greater than C_{10} that possesses a terminal carboxyl group.

long-chain-fatty-acid–CoA ligase EC 6.2.1.3; *other names*: acyl-activating enzyme; acyl-CoA synthetase; fatty acid thiokinase (long-chain); lignoceroyl-CoA synthase; an enzyme that catalyses the reaction between ATP and a long-chain carboxylic acid and CoA to form an acyl-CoA with release of AMP and pyrophosphate. It activates free fatty acids formed, e.g., by phospholipase action for further metabolism. Examples from yeast: long-chain-fatty-acid–CoA ligase 1 (long-chain acyl-CoA synthetase 1; fatty acid activator 1): database code LCF1_YEAST, 700 amino acids (77.78 kDa); long-chain-fatty-acid–CoA ligase 2 (long-chain acyl-CoA synthetase 2; fatty acid activator 2): database code LCF2_YEAST, 744 amino acids (83.34 kDa); long-chain-fatty-acid–CoA ligase 3 (long-chain acyl-CoA synthetase 3; fatty acid activator 3): database code LCF3_YEAST, 694 amino acids (77.86 kDa).

long-chain-3-hydroxyacyl-CoA dehydrogenase EC 1.1.1.211; *other name*: β-hydroxyacyl-CoA dehydrogenase; an enzyme of the **beta-oxidation system** that catalyses the oxidation by NAD^+ of (*S*)-3-hydroxyacyl-CoA to 3-oxoacyl-CoA with the formation of NADH. *See* **3-hydroxyacyl-CoA dehydrogenase**.

longitudinal relaxation time *an alternative name for* **spin-lattice relaxation time**.

long-patch repair *see* **short-patch repair**.

long-range interaction describing an interaction between residues that are situated relatively far apart in a polypeptide or polynucleotide sequence.

long terminal repeat *abbr.*: LTR; a double-stranded DNA sequence, generally several hundred base pairs long, that is repeated at the two ends of the DNA of retroviruses and retrotransposons.

loop **1** the round or oval figure produced by a line, wire, thread, etc. that curves round to cross (or nearly cross) itself. **2** *(in electronics)* any closed electric or magnetic circuit through which a signal can circulate. **3** *(in computing)* any set of instructions in a program that is carried out repeatedly until some specified condition is satisfied.

loopback DNA *an alternative name for* hairpin DNA; *see* **hairpin**.

loop injector a device for introducing samples into a high-pressure liquid chromatographic column without interruption of the solvent flow to the column. It consists of a loop of metal tubing of small volume, which is filled with the sample; this can then, by an appropriate valve, be flushed by eluent directly onto the column.

loop of Henle *or* **Henle's loop** the U-shaped part of a nephron lying in the renal medulla. It comprises a thin descending tubule and an ascending tubule formed of both a thin and a

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thick segment. It plays a role in the selective reabsorption of fluid and solutes. [After Friedrich Gustav Jakob Henle (1809–85), German anatomist and pathologist.]

lophotoxin a cyclic diterpenoid, isolated from Pacific gorgonians (sea fans and whips) of the genus *Lophogorgia*, that irreversibly inactivates the nicotinic acetylcholine receptor on intact BC3H-1 cells.

Lorentz correction factor a correction factor for the effect of solvent polarizability on optical rotation by solutions of proteins or other macromolecules. It is given by: $3/(n^2 + 2)$, where n is the refractive index of the solvent. [After Hendrik Antoon Lorentz (1853–1928).]

Lorentzian lineshape function an equation for the lineshape of a nuclear magnetic resonance absorption signal:

$$g(\omega) = T_2/[1 + (\omega - \omega_0)^2 T_2^2],$$

where $g(\omega)$ is a measure of the intensity of the resonance at a frequency ω, ω_0 is the actual Larmor frequency of the resonating nucleus, and T_2 is the spin–spin relaxation time.

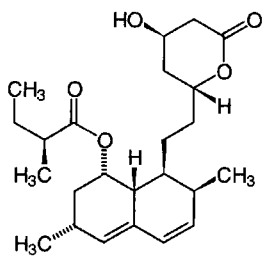
loricrin the major protein of the cornified cell envelope of terminally differentiated epidermal keratinocytes. It is a substrate for transglutaminase, and exists as monomers cross-linked by disulfide and *N*-(γ-glutamyl)lysine isodipeptide bonds. Example from human: database code LORI_HUMAN, 316 amino acids (26.01 kDa).

losartan 2-butyl-4-chloro-1-(*p*-(*O*-1*H*-tetrazol-5-ylphenyl)benzyl)imidazol-5-methanol; an antihyperactive drug that blocks the binding of angiotensin II (*see* **angiotensin**) to the AT_1 receptor. Affinity for this receptor is much greater than for the AT_2 receptor. It is oxidized by a cytochrome P450 to a carboxylic-acid metabolite that is largely responsible for most of its angiotensin II antagonistic effects.

Loschmidt constant *symbol*: N_L; the number of molecular entities in unit volume of an ideal gas at 1 atm and 273.15 K. It is equal to the **Avogadro constant** divided by the molar volume, and has the value $2.686\,763 \times 10^{25}$ m^{-3}. [After Josef Loschmidt (1821–95), Austrian physicist.]

Loschmidt number *or* **Loschmidt's number** the numerical value of the **Loschmidt constant**.

lovastatin *or* **mevinolin** 6α-methylcompactin; a metabolite from some fungi (e.g. *Monascus ruber*, *Aspergillus terreus*) that is a potent inhibitor of **hydroxymethylglutaryl-CoA reductase**. It is useful clinically as an antihypercholesterolemic; it reduces plasma levels of total low-density-lipoprotein (LDL), and very-low-density-lipoprotein cholesterol, but it can increase high-density-lipoprotein cholesterol. Its effects result in the induction of up-regulation of LDL receptors on hepatocytes. Two proprietary names are: Mevacor; Mevinacor.



low-complexity region a region in the amino-acid sequence of a protein in which a particular amino acid or a small number of different amino acids are enriched. *See*, for example, **leucine zipper**.

low-density lipoprotein *abbr.*: LDL; one of the classes of lipoproteins found in blood plasma in many animals (data normally relate to humans). LDLs are also known as β lipoproteins due to their electrophoretic mobility intermediate between high-density or α lipoprotein, and the origin. LDL particles have diameter 19.6–22.7 nm, solvent density for isolation (g mL^{-1}) 1.019–1.063, hydrated density (g mL^{-1}) 1.034. Their approximate composition (% by weight) is 13% unesterified cholesterol, 39% esterified cholesterol, 17% phospholipid, 11% triacylglycerol, 20% protein. Their apolipoprotein composition (% by weight total apolipoprotein) is 98% B-100 with traces of different C and E apolipoproteins. They are synthesized in plasma from very-low-density lipoproteins and intermediate density lipoproteins through the action of lipoprotein lipase; they transport cholesterol to peripheral tissues. They have the highest content of cholesterol of any plasma lipoprotein, and have been linked to the incidence of coronary heart disease in epidemiological studies. *See also* **apolipoprotein** (for individual apolipoproteins), and **LDL receptor**.

low-density-lipoprotein receptor *see* **LDL receptor**.

low-energy compound a name sometimes applied improperly to certain compounds that undergo reaction leading to release or transfer of, e.g., phosphate, where the standard free energy change for the hydrolysis of the bond is <20 kJ mol^{-1}. It is used especially in making a distinction from a **high-energy compound**. The use of the term does not meet the highest standards of thermodynamic correctness.

low-lipid lipoprotein *(sometimes) an alternative name for* **high-density lipoprotein**.

Lowry method a colorimetric method for the estimation of small amounts (down to 10 μg) of protein. It is a combination of the **biuret reaction** for peptide bonds and the colour formed by reaction of **Folin–Ciocalteau reagent** with tyrosine and tryptophan residues in the protein. [After Oliver Howe Lowry (1910–1996), US pharmacologist and biochemist.]

low-spin complex any of the ligand complexes of transition-metal ions having a maximal number of paired *d*- or *f*-shell electrons in the lower energy levels. This state occurs when the pairing energy is less than the crystal-field splitting energy. *Compare* **high-spin complex**.

LPG *abbr. for* lipophosphoglycan (*see* **GPI anchor**).

LPH *abbr. for* lipotropic hormone (i.e. **lipotropin**).

LPL *abbr. for* lipoprotein lipase.

LPS *abbr. for* **1** lipopolysaccharide. **2** lipase (def. 2).

Lr *symbol for* lawrencium.

L region any region in a (carcinogenic) polycyclic aromatic hydrocarbon that consists of two *para*-carbon atoms, e.g. the *meso*-9,10-carbon atoms of anthracene, which display the highest free-valence indices. The lack of such a region has been suggested to correlate with a lack of carcinogenicity of some hydrocarbons. *Compare* **K region**.

LRF *abbr. for* luteinizing hormone releasing factor (*see* **gonadotropin-releasing hormone**).

LRH *abbr. for* luteinizing hormone releasing hormone (*see* **gonadotropin-releasing hormone**).

LRR *abbr. for* leucine-rich repeat.

LSC *abbr. for* **1** liquid-scintillation counting. **2** liquid–solid chromatography.

LSD *abbr. for* lysergic acid diethylamide; *see* **lysergic acid**.

L7/L12 site a component of EF-Tu translocase (*see* **EF-T**) activity involving in bacteria the **ribosomal proteins** L7 and L12.

L strand *abbr. for* light strand.

LT *abbr. for* **1** leukotriene; the subtype may be indicated by a third letter, as in LTA (leukotriene A). **2** lymphotoxin.

LTR *abbr. for* long terminal repeat.

L-type pentose pathway *see* **pentose phosphate pathway**.

Lu *symbol for* lutetium.

Lubrol *a proprietary name for* a polyoxyethylene nonionic detergent; the structure of Lubrol PX is the same as $C_{12}E_9$ (see C_xE_y). It is useful for solubilizing membrane-bound enzymes such as adenylate cyclase.

luciferase any member of a group of monooxygenase enzymes that catalyse bioluminescent reactions. **Firefly luciferase** (EC 1.13.12.7; *recommended name*: *Photinus* luciferin 4-monooxygenase (ATP hydrolysing)) occurs in the lantern of the American firefly, *Photinus pyralis*, and may be used with firefly

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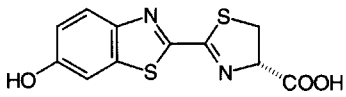
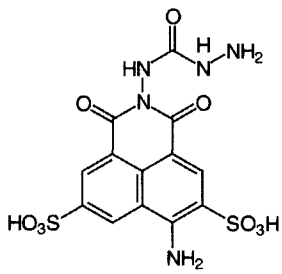
luciferin for estimation of low concentrations (10^{-6}–10^{-10} mol L^{-1}) of ATP. It catalyses a reaction between *Photinus* luciferin, O_2, and ATP to form oxidized *Photinus* luciferin, CO_2, H_2O, AMP, pyrophosphate, and $h\nu$; magnesium is a cofactor. It covalently binds the adenylyl group (AMP) after reaction with ATP and release of pyrophosphate. It is a peroxisomal enzyme. Example from *Luciola lateralis* (firefly): database code LUCI_LUCLA, 548 amino acids (60.06 kDa). **Bacterial luciferase** (EC 1.14.14.3; *recommended name*: alkanal monooxygenase (FMN-linked)) occurs in *Photobacterium fischeri* and catalyses a reaction between RCHO, reduced FMN, and O_2 to form RCOOH, FMN, H_2O, and $h\nu$. It may be used together with NAD(P)H dehydrogenase (FMN), EC 1.6.8.1, from luminescent bacteria for estimation of low concentrations (10^{-7}–10^{-9} mol L^{-1}) of NAD(P)H. For examples *see* **Lux proteins**.

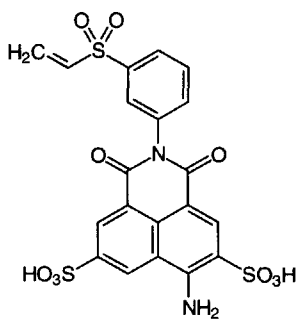
luciferin any bioluminescent substance that is a substrate for a **luciferase** enzyme. Luciferins from different sources often bear no structural resemblance to one another. Firefly luciferin, obtained from the lantern of the American firefly, *Photinus pyralis*, is D-(–)-4,5-dihydro-2-(6-hydroxy-2-benzothiazoloyl)-4-thiazolecarboxylic acid.



Lucifer Yellow one of several dyes based on the structure 6-amino-2,3-dihydro-1,3-dioxo-benz[*d*,*e*]isoquinoline-5,8-disulfonic acid. Lucifer Yellow CH has been used as a marker for movement between cells, and for ultrastructure tracing; Lucifer Yellow VS covalently labels proteins rapidly under mild conditions.



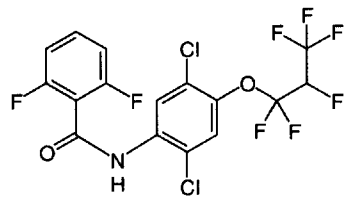
Lucifer Yellow CH



Lucifer Yellow VS

Lucite *a proprietary name for* **poly(methyl methacrylate)**.

lufenuron *N*-[2,5-dichloro-4-(1,1,2,3,3,3-hexafluoropropoxy)-phenylaminocarbonyl]-2,6-difluorobenzamide; an inhibitor of insect development, used as a once-per-month pill to control flea populations on domestic dogs, by inhibiting egg development.

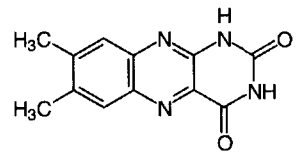


luffin a type I **ribosome-inactivating protein**.

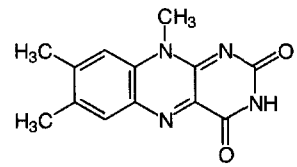
luliberin *the recommended name for* a hypothalamic decapeptide amide now known to be identical with **gonadotropin-releasing hormone**.

lumen **1** (*pl.* **lumens**) *symbol*: lm; the SI derived unit of **luminous flux**, equal to the quantity of visible electromagnetic radiation emitted per second in a cone of unit solid angle (one steradian, sr) by a uniform point source of unit luminous intensity (one candela, cd); i.e. 1 lm = 1 cd sr. **2** (*pl.* **lumina**) the cavity or passageway of a tubular organ, such as a blood vessel, duct, or length of gut. **3** the volume enclosed within the membranes of a mitochondrion or of the endoplasmic reticulum, or of microsomes prepared from cells. **4** the space enclosed by the walls of a plant cell that no longer contains a protoplast. **5** the bore of a catheter, hollow needle, or other tubular device. —**luminal** *adj.*

lumichrome 7,8-dimethylalloxazine; a compound showing a blue fluorescence, formed by the photolysis of riboflavin in acid or neutral solution.



lumiflavin 7,8,10-trimethylisoalloxazine; a compound showing a yellow-green fluorescence, formed by the photolysis of riboflavin in alkaline solution.



lumina *the plural of* **lumen** (def. 2).

luminal proteins *or (sometimes)* **ER-resident proteins** proteins that are retained within the cisternae of the **rough endoplasmic reticulum**, e.g protein disulfide isomerase. Such proteins possess at their C terminus four characteristic amino acids, Lys-Asp-Glu-Leu (**KDEL**) in animal cells and His-Asp-Glu-Leu (**HDEL**) in yeast. The proteins move to the Golgi and are returned to the endoplasmic reticulum.

luminescence the production of visible light by any mechanism that does not depend upon the system having a temperature appreciably above the ambient. It comprises **fluorescence** and **phosphorescence**. —**luminescent** *adj.*

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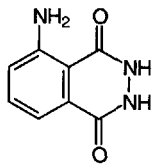
luminogenic 1 producing **luminescence**. 2 of or pertaining to a nonluminescent material that can be acted on by an enzyme to produce a luminescent substance.

luminol 5-amino-2,3-dihydro-1,4-phthalazinedione; a substance useful in the detection or determination of trace amounts of oxidizing agents by virtue of the intense bluish luminescence it emits on oxidation in alkaline solution.



luminometer an instrument for measuring **luminescence**. Given appropriate conditions, it may be used also to measure the concentrations of enzymes, substrates, etc. that participate in, or can be coupled to, light-producing reactions.

luminometry the measurement of **luminescence** with a luminometer. —**luminometric** *adj.*

luminophore 1 any luminescent substance, whether a fluor or a phosphor. 2 a molecular grouping responsible, or thought to be responsible, for the **luminescence** of a larger molecule; a luminescent chromophore.

luminous 1 emitting visible light; bright, shining. 2 *(in photometry)* (of a physical quantity relating to light) evaluated by the visual sensation of brightness to the eye of an observer rather than by an absolute measurement of radiant energy.

luminous flux *symbol*: Φ_v *or* Φ *or* P_v *or* P; a measure of the rate of flow of radiant energy within the visible region of the electromagnetic spectrum. The SI derived physical quantity is the arithmetic product of the **luminous intensity** of a source of visible light and the solid angle, expressed in steradians, into which the light is emitted. The SI derived unit of luminous flux is the **lumen** (def. 1).

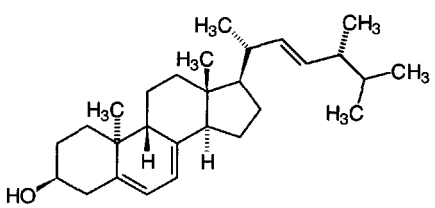
luminous flux density the **luminous flux** per unit cross-sectional area of a beam of light.

luminous intensity *symbol*: I_v *or* I; one of the seven SI base physical quantities, defined as the amount of visible light emitted per second per steradian by a point source in a given direction. The SI base unit of luminous intensity is the **candela**.

lumirhodopsin an intermediate in the light-induced modification of **rhodopsin** prior to its breakdown into opsin and all-*trans*-retinal. It has an absorption maximum at 497 nm.

lumisome a membrane-bound particle, ≈200 nm in diameter and isolable from homogenates of various species of luminescent marine coelenterates, that contains all the proteins necessary for the production of the typical green bioluminescence observable *in vivo*. It is probably the cytoplasmic organelle responsible for emission of light by such organisms.

lumisterol 9β,10α-ergosta-5,7,22-trien-3β-ol; a compound produced by the UV irradiation of **ergosterol**, from which it differs in the spatial arrangement of the methyl group at C-10.



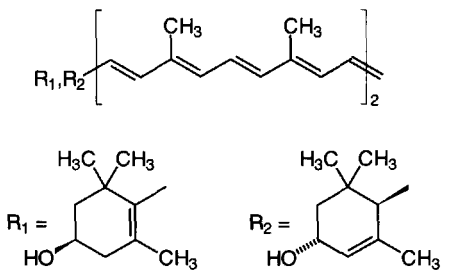
Lundh test a test for pancreatic function in which the pancreas is stimulated by a test meal (corn oil, milk powder, and glucose), after which trypsin activity is measured in duodenal juice.

Luria, Salvador Edward (1912–91), Italian-born US physician and biologist, Nobel Laureate in Physiology or Medicine (1969) jointly with M. Delbrück and A. D. Hershey 'for their discoveries concerning the replication mechanism and the genetic structure of viruses'.

luteal of, relating to, or characterized by the development of a corpus luteum or corpora lutea.

luteal phase *see* **estrous cycle**.

lutein 3,3′-dihydroxy-α-carotene, one of the most widespread naturally occurring xanthophylls (i.e. carotene alcohols; *see* **carotenoid**), found in many higher plants, some algae, egg yolk, and corpora lutea.



luteinize *or* **luteinise** to cause the formation of corpora lutea in; to undergo transformation into a corpus luteum. —**luteinization** *or* **luteinisation** *n.*

luteinizing hormone *or* **luteinising hormone** *abbr.*: LH; one of the two gonadotropic **glycoprotein hormones** secreted by the anterior pituitary. Of molecular mass 28.5 kDa (human), it consists of α and β subunits, the α subunit being almost identical within a given species to that of other glycoprotein hormones and the β subunit conferring hormonal specificity; the carbohydrate content is 15.5% (human). In the female it promotes ovulation and luteinization of the ovarian follicle, where it stimulates the conversion of progesterone to pregnenolone, thereby increasing the formation of further progesterone. In the male it stimulates testicular interstitial (Leydig) cell function by promoting the production of androgens, especially testosterone. Example, β chain (precursor) from *Bos taurus*: database code LSHB_BOVIN, 141 amino acids (15.20 kDa). *Recommended name*: lutropin; *former name*: interstitial cell-stimulating hormone (*abbr.*: ICSH).

luteinizing hormone/follicle-stimulating hormone releasing factor *abbr.*: LH/FSH-RF *see* **gonadotropin-releasing hormone**.

luteinizing hormone releasing factor *abbr.*: LHRF *see* **gonadotropin-releasing hormone**.

luteinizing hormone releasing hormone *abbr.*: LHRH *or* LH-RH *or* LRH; *see* **gonadotropin-releasing hormone**.

luteo+ *comb. form* indicating 1 yellow. 2 of the **corpus luteum**.

luteolysin *an alternative name for* **prostaglandin** $F_{2\alpha}$.

luteolysis degeneration or regression of the **corpus luteum**. —**luteolytic** *adj.*

luteotropic hormone *or* **luteotrophic hormone** *abbr.*: LTH; *a former name for* **prolactin**.

luteotropin *or* **luteotrophin** *a former name for* **prolactin**.

lutropin *the recommended name for* **luteinizing hormone**.

lux *symbol*: lx; the SI derived unit of illuminance, equal to 1 lumen per square metre; i.e. 1 lx = 1 lm m^{-2}.

Lux proteins the counterpart in marine bacteria of the **luciferase** system. They mediate bioluminescence and are products of genes regulated by the *lux* operon. Examples are from *Vibrio* spp. LuxA (catalytic subunit) and LuxB constitute bacterial luciferase (EC 1.14.14.3). It catalyses a reaction between reduced FMN, RCHO, and O_2 to form FMN, RCOOH, H_2O, and *hν*. Examples from *V. fischeri*: LUXA, database code LUXA_VIBFI, 354 amino acids (40.30 kDa); LUXB, database

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code LUXB_VIBFI, 326 amino acids (37.31 kDa). LuxC is an **acyl-CoA reductase** required to form the 'RCHO' above. Example from *V. harveyi*: database code LUXC_VIBHA, 477 amino acids (54.78 kDa). LuxD is an acyl transferase component of the fatty acid reductase system required for aldehyde biosynthesis (EC 2.3.1.–). Example from *V. harveyi*: database code LUXD_VIBHA, 305 amino acids (34.17 kDa). LuxE is an acyl-protein synthetase (EC 6.2.1.19) that activates tetradecanoic acid. LuxG is the flavin reductase (EC 1.–.–.–), Example from *V. fischeri*: database code LUXG_VIBFI, 236 amino acids (26.47 kDa). LuxI and LuxJ are part of the regulatory system; they are required for the synthesis of OHHL (*N*-(3-oxohexanoyl)-L-homoserine lactone), an autoinducer molecule that binds to LuxR. Example from *V. fischeri*: database code LUXJ_VIBFI, 193 amino acids (21.99 kDa). LuxR is the transcriptional activator. Example from *V. fischeri*: database code LUXR_VIBFI, 250 amino acids (28.52 kDa).

LVP *abbr. for* lysine vasopressin.

LW antigen *abbr. for* Landsteiner–Weiner antigen. *See* **Rhesus factor**.

Lwoff, André Michel (1902–94), French microbiologist; Nobel Laureate in Physiology or Medicine (1965) jointly with F. Jacob and J. L. Monod 'for their discoveries concerning genetic control of enzyme and virus synthesis'.

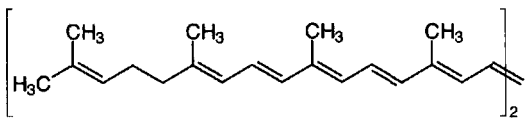
lx *symbol for* lux.

LX *abbr. for* lipoxin.

lyase **1** *the systematic name for* any enzyme of EC class 4 that catalyses the cleavage of C–C, C–O, C–N, and other bonds, leaving double bonds, or conversely adding a group to a double bond. **2** **17,20-lyase** *the common name for* 17α-hydroxyprogesterone aldolase (EC 4.1.2.30).

lyate ion the anion produced by the autoprotolysis of a protogenic solvent; e.g. the hydroxide ion is the lyate ion of water.

lycopene the characteristic red pigment of tomatoes and some other ripe fruit. It is an acyclic carotenoid, and the biosynthetic precursor of the cyclic carotenes in plants.



lycopodium **1** any clubmoss of the genus *Lycopodium*. **2** the spores of various clubmosses, e.g. *L. clavatum*. They are used as a covering for pills and suppositories, in pyrotechnics, and in foundry work.

lymph **1** the pale-yellow, clear, or cloudy fluid that is contained within the vessels of the **lymphatic system**. It contains a little protein, and derives from the interstitial fluid, which is drained by the lymphatic vessels and ultimately discharged into the bloodstream, e.g. via the thoracic duct. The composition of lymph varies in different parts of the body, that from the liver and intestine containing more protein, and the latter more fat in the form of chylomicrons. Lymph also contains varying numbers of cells, mostly small lymphocytes, and coagulation factors. **2** the exudation from a sore.

lymphatic **1** of, pertaining to, or containing lymph; of or pertaining to the lymphatic system. **2** a lymphatic vessel.

lymphatic system the extensive network of capillary-like lymphatic vessels in vertebrates that convey the lymph from the peripheral tissues to the venous system. **Lymph nodes** occur at various points along the vessels.

lymph node *or* **lymph gland** any of numerous small swellings distributed throughout the lymphatic system of vertebrates. Each node consists largely of lymphocytes, together with macrophages and dendritic cells held together in a loose reticulum. Lymph nodes receive lymph from the peripheral tissues via afferent lymphatic vessels and pass it on via efferent vessels to more centrally placed lymph nodes, and ultimately to the thoracic duct. The lymph nodes act as filters through which the lymph must pass and where foreign material comes into intimate contact with macrophages and lymphocytes. They are active centres for phagocytosis and the site of initiation of humoral and cell-mediated immune reactions.

lympho+ *or (before a vowel)* **lymph+** *comb. form* indicating lymph or the lymphatic system.

lymphoblast any **blast cell** of the **lymphoid cell series**. —**lymphoblastic** *adj.*

lymphocyte a type of **leukocyte** found in vertebrates and having various functions in specific immunity. A lymphocyte is a spherical cell, 7–12 μm in diameter, with a large, round nucleus, often indented when seen by electron microscopy, and scanty cytoplasm containing scattered ribosomes but little endoplasmic reticulum and few other organelles. Lymphocytes occur in lymph nodes, other tissues, lymph, and blood, and they circulate between these tissues. Mature, differentiated lymphocytes comprise two main classes, **B lymphocytes** and **T lymphocytes**. Lymphocytes without the characteristics of either of these classes are termed **null lymphocytes**.

lymphocyte-activating factor *abbr.*: LAF; *an alternative name for* **interleukin 1**.

lymphocyte transformation *see* **transformation** (def. 3).

lymphocytosis an abnormal increase in the number of lymphocytes, especially in blood.

lymphoid of or resembling lymph, or lymphatic tissue.

lymphoid cell series a cell series comprising all cells that morphologically resemble **lymphocytes**, their precursors (e.g. lymphoblasts), and cells that may be derived from them (e.g. plasma cells).

lymphoid tissue any vertebrate tissue that is made up predominantly of **lymphocytes**, e.g. lymph, lymph nodes, spleen, thymus, Peyer's patches, adenoids, pharyngeal tonsils, and, in birds, bursa of Fabricius and cecal tonsils.

lymphokine any member of a varied group of nonimmunoglobulin, soluble factors released by primed lymphocytes on a second interaction with the specific activator (which may be a soluble antigen, a cell-associated antigen, or a mitogen). They play a role in **cell-mediated immunity** by modulating the behaviour of other types of cell within the same organism (e.g. macrophages, polymorphonuclear leukocytes), and are now considered to be a subgroup of the **cytokines**. Specific lymphokines include: chemotactic factor for macrophages, lymphotactin, lymphotoxin (i.e. **tumour necrosis factor** β), macrophage-activating factor (MAF), macrophage migration enhancement factor, **macrophage migration inhibitory factor** (MIF), (antigen-independent) mitogenic factor, skin-reactive factor, and **transfer factor**. Lymphokines that can act between different populations of leukocytes are known also as **interleukins**. *See also* **colony-stimulating factor**.

lymphoma any malignant tumour, or condition allied to a tumour, arising from some or all of the cells of lymphoid tissue. The term includes lymphatic leukemias, Hodgkin's disease, and reticuloses.

lymphoreticular tissue *an old general term for* tissues consisting largely of lymphocytes and macrophages.

lymphotoxin *abbr.*: LT; *an alternative name for* **tumour necrosis factor** β; *see also* **lymphokine**.

LYN a protooncogene encoding a **tyrosine kinase** belonging to the ***src*** family: Database code KLYN_HUMAN, 512 amino acids (58.51 kDa).

Lynen, Feodor (1911–79), German biochemist, Nobel Laureate in Physiology or Medicine (1964) jointly with K. E. Bloch 'for their discoveries concerning the mechanism and regulation of the cholesterol and fatty acid metabolism'.

lyo+ *comb. form* indicating looseness, dispersion, or dissolution.

lyochrome *a former name for* **flavin**.

lyocytosis cell lysis by extracellular digestion, e.g. during insect metamorphosis.

lyoenzyme *an old term for* any enzyme existing in the cell in soluble form.

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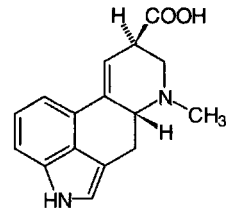
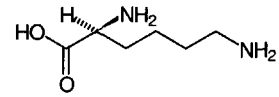
lyoglycogen *an old name for* the fraction of a sample of glycogen that is extractable by water on a steam bath.
lyolysis *an alternative term for* **solvolysis**.
Lyon hypothesis *(in genetics)* the hypothesis that gene dosage compensation in mammals is accomplished by random inactivation of one of the two X chromosomes in all somatic cells of females. [After Mary Francis Lyon (1925–), British geneticist.]
lyonium ion any cation produced by the protonation of a solvent molecule, e.g. H_3O^+, $CH_3OH_2^+$.
lyophile **1** *(in chemistry)* a **lyophilic** compound. **2** having lyophilic properties.
lyophilic *or* **lyophile** (of a substance or surface) solvent preferring; easily wetted or solvated by the solvent present; the term comprehends **hydrophilic** when the solvent is water. *Compare* **lyophobic**.
lyophilic sol any sol in which the disperse phase has an attraction for the continuous phase.
lyophilization *or* **lyophilisation** strictly, the process of rendering lyophile or lyophilic. The term is now usually specifically applied to freeze-drying in which, by use of a vacuum, water is removed from ice by sublimation. This use bears little relationship to the true meaning of lyophile, except in so far as it maintains proteins subjected to it in a lyophilic state. — **lyophilize** *or* **lyophilise** *vb.*
lyophilizer*or* **lyophiliser** an apparatus for effecting lyophilization; a freeze-drier.
lyophobic *or* **lyophobe** (of a substance or surface) solvent rejecting; resistant to being wetted or solvated by the solvent present; the term comprehends **hydrophobic** when the solvent is water. *Compare* **lyophilic**.
lyophobic sol any sol in which the disperse phase has no attraction for the continuous phase. Lyophobic sols cannot be formed by spontaneous dispersion in the medium.
lyotropic *or* **lyotrope** of or associated with the difference between the internal pressure of a solution compared with that of the solvent caused by the solute.
lyotropic mesophase any mesophase (i.e. **liquid crystal**) whose phase transitions are readily effected by changes in concentration.
lyotropic series *or* **Hofmeister series** a series of ions arranged in order of their **lyotropic** effects, especially their ability to cause precipitation of a lyophilic sol (to salt-out).
lypressin *see* **[8-lysine]vasopressin**.
Lys *symbol for* a residue of the α-amino acid L-lysine (alternative to K).
lys+ *a variant form of* **lyso+** (before a vowel).
lysate any solution or other preparation containing the products of **lysis** of cells. The term is applied especially to lysed bacterial or blood cells.
+lysate *comb. form* denoting a mixture resulting from decomposition, breakdown, or lysis (of or by something indicated); e.g. autolysate, cytolysate, hemolysate, hydrolysate.
Lys-bradykinin *abbr. for* lysylbradykinin (i.e. kallidin); *see* **bradykinin**.
lyse to effect **lysis** (of a cell, etc.); to undergo lysis.
+lyse *comb. form* denoting decompose, breakdown, or lyse (of or by something indicated); e.g. autolyse, cytolyse, electrolyse, hemolyse, hydrolyse.
lysergamide lysergic acid amide. All known **ergot alkaloids** are derivatives of D-lysergamide, the simplest being **ergonovine**.
lysergic acid 9,10-didehydro-6-methylargoline-8β-carboxylic acid an alkaloid obtained from **ergot**; it is a tetracyclic indole derivative. Lysergic acid diethylamide (*abbr.*: LSD) is a powerful hallucinogenic substance. (Illustrated top right.)
lysin any agent, such as an antibody, enzyme, toxin, etc., that is able to lyse cells.
+lysin *comb. form* denoting an (indicated) agent that effects, or can effect, lysis, specifically the lysis of cells (cytolysis).
lysinate **1** lysine anion; the anion, $H_2N–[CH_2]_4–CH(NH_2)–COO^-$, derived from **lysine**. **2** any salt containing lysine anion. **3** any ester of lysine.



lysergic acid

lysine *the trivial name for* α,ε-diaminocaproic acid; 2,6-diaminohexanoic acid; $H_2N–[CH_2]_4–CH(NH_2)–COOH$; a chiral α-amino acid. L-Lysine (*symbol*: K *or* Lys), (*S*)-2,6-diaminohexanoic acid, is a coded amino acid found in peptide linkage in proteins; codon: AAA or AAG. In mammals it is an essential dietary amino acid and is ketogenic. D-Lysine (*symbol*: D-Lys *or* DLys), (*R*)-2,6-diaminohexanoic acid, is a substrate for **lysine racemase** and D-lysine 5,6-aminomutase. The conversion of D-lysine to L-pipecolic acid, and of the latter to L-lysine, occurs in *Nicotiana glauca* and in *Neurospora crassa*.



L-lysine

D-lysine 5,6-aminomutase EC 5.4.3.4; *other name*: D-α-lysine mutase; an enzyme that catalyses the reaction:

D-lysine = 2,5-diaminohexanoate;

cobalamin is a cofactor.
lysine(arginine) carboxypeptidase EC 3.4.17.3; *other names*: carboxypeptidase N; arginine carboxypeptidase; kininase I; anaphylotoxin inactivator; an enzyme that hydrolyses peptidyl-L-lysine (or L-arginine) to peptide and L-lysine (or L-arginine). It inactivates bradykinin complement components, C3a and C5a by removal of the C-terminal Arg. Example (precursor) from human: database code CBPN_HUMAN, 458 amino acids (52.23 kDa).
lysine (base) a lysine residue when the ε-amino group is unprotonated.
lysine hydroxylase *see* **procollagen-lysine 5-dioxygenase**.
lysine intolerance a genetically determined metabolic defect of humans in which the ingestion of relatively large amounts of lysine (in protein) causes hyperlysinemia, hyperammonemia, and coma. It is possibly attributable to deficient activity of lysine dehydrogenase (L-lysine:NAD^+ oxidoreductase, EC 1.4.1.15).
lysine 6-monooxygenase *see* **monoxygenase**.
lysine racemase EC 5.1.1.5; an enzyme catalysing the reaction:

L-lysine = D-lysine.

lysine vasopressin *see* **[8-lysine]vasopressin**.
[8-lysine]vasopressin *abbr.*: [Lys^8]vasopressin; *nonproprietary name*: lypressin; the molecular form of **vasopressin** in which the variable eighth position in its amino-acid sequence is occupied by a lysine residue. This is the form of the hormone present in pigs and a few other related mammals. It is sometimes incorrectly designated as lysine vasopressin.
lysinium **1** *the usual term for* lysinium(1+); the monocation of **lysine**. In theory, the term denotes any ion or mixture of ions formed from lysine and having a net charge of +1, although the species $H_3N^+–[CH_2]_4–CH(NH_3^+)–COO^-$ generally predominates in practice. **2** *the systematic name for* lysinium(2+); the dication of lysine.

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lysino 1 **N^2-lysino** the alkylamino group, H_2N–$[CH_2]_4$–CH(COOH)–NH–, derived from lysine by loss of a hydrogen atom from its α-amino group. 2 **N^6-lysino** the alkylamino group, HOOC–$CH(NH_2)$–$[CH_2]_4$–NH–, derived from lysine by loss of a hydrogen atom from its ε-amino group.

lysis 1 *(in chemistry)* the breaking down of a substance by the splitting of its molecules into two parts; the rupture of a covalent bond. 2 *(in biology)* the disintegration of cells or cell organelles by rupture of their outer membranes. 3 *(in medicine)* the gradual diminution in the severity of the symptoms of a disease; remission.

+lysis *comb. form* denoting breaking down, decomposition, disintegration, or dissolution. The first element of the word may indicate: (1) the agent, e.g. electrolysis, hydrogenolysis, biolysis; (2) the substance or object affected, e.g. glycolysis, lipolysis; or (3) some other characteristic, e.g. autolysis, catalysis, heterolysis, homolysis. —**+lytic** *adj.*

lyso+ *or (before a vowel)* **lys+** 1 *comb. form* indicating a dissolving or loosening; denoting lysis or the products of lysis. 2 *prefix* (to the name of a phospholipid) denoting removal of one of its two acyl groups; a locant may be used to designate the site of (hydro)lysis, e.g. 2-lyso designates deacylation at position 2. The term originated from the fact that such compounds are hemolytic, but it is now used to indicate a limited deacylation.

lysochrome any substance that will dissolve in lipids and colour them.

lysogen 1 any **lysogenic bacterium**. 2 any antigen that stimulates **lysin** production.

lysogenesis 1 *an alternative term for* **lysogeny**. 2 the production of a lysin or lysis.

lysogenic 1 pertaining to, or capable of producing or undergoing **lysis** (def. 1). 2 of, or relating to **lysogeny**. —**lysogenicity** *n.*

lysogenic bacterium any bacterium carrying a temperate bacteriophage as a **prophage** integrated into the bacterial genome. It has the potential to produce and release infective bacteriophages as a stable, heritable trait, which may become activated spontaneously or in response to certain stimuli. Moreover, it is immune to lytic infection by the same or closely related phages.

lysogenic conversion *see* **bacteriophage conversion**.

lysogenic virus any virus capable of becoming a **prophage**.

lysogenize *or* **lysogenise** to convert a nonlysogenic bacterial strain into a lysogenic strain by infection with a temperate bacteriophage, with resultant incorporation of the phage into the bacterial genome. —**lysogenization** *or* **lysogenisation** *n.*

lysogeny *or* **lysogenesis** the state created in a bacterial cell when the prophage of a temperate bacteriophage is incorporated into the bacterial genome as a stable, heritable character. Such a cell can be activated to produce and release mature phage, with accompanying cell lysis. *See also* **lysogenic bacterium**.

Lys(5-OH) *symbol for* a residue of the α-amino acid 5-hydroxy-L-lysine (less-preferred alternative to Hyl or 5Hyl).

Lysol *the proprietary name for* a disinfectant consisting of a mixture of *o*-, *m*-, and *p*-cresols solubilized with an excess of a potassium soap.

lysolecithin *a former name for* **lysophosphatidylcholine**.

lysolecithin acyltransferase *see* **1-acylglycerophosphocholine O-acyltransferase**.

lysophosphatidic acid any **phosphatidic acid** deacylated at positions 1 or 2.

lysophosphatidyl any **phosphatidyl** group deacylated at positions 1 or 2.

lysophosphatidylcholine *or (formerly)* **lysolecithin** any **phosphatidylcholine** (i.e. lecithin) deacylated at positions 1 or 2.

lysophospholipid any **phospholipid** deacylated at positions 1 or 2.

lysoplasmenic acid any derivative of *sn*-glycero-3-phosphate that has an *O*-(1-alkenyl) residue on carbon-1, the hydroxyl group in position 2 being unsubstituted.

lysoplasmenyl any **plasmenyl** group in which the hydroxyl group in position 2 is unsubstituted.

lysosomal carboxypeptidase B *see* **cysteine-type carboxypeptidase**.

lysosomal carboxypeptidase C *see* **lysine pro-X carboxypeptidase**.

lysosomal Pro-X carboxypeptidase EC 3.4.16.2; *other names*: proline carboxypeptidase; angiotensinase C; lysosomal carboxypeptidase C; an enzyme that catalyses the cleavage of a Pro-|-Xaa bond to release a C-terminal amino acid. Example from human: database code A47352, 496 amino acids (55.74 kDa).

lysosomal storage disease any of a group of hereditary diseases, with widely varying manifestations, in which there is deficiency of a single lysosomal enzyme associated with abnormal deposits (of substrate) within membrane-bound vesicles. The group is subdivided into the following classes: type II **glycogen disease**, **mucopolysaccharidoses**, sphingolipidoses, **mucolipidoses**, and a few others.

lysosome any of a group of related cytoplasmic, membrane-bound organelles that are found in most animal cells and that contain a variety of hydrolases, most of which have their maximal activities in the pH range 5–6. The contained enzymes display latency if properly isolated. About 40 different lysosomal hydrolases are known and lysosomes have a great variety of morphologies and functions. —**lysosomal** *adj.*

lysostaphin EC 3.5.1.–; an enzyme that hydrolyses polyglycine links in peptidoglycans. Zinc is a cofactor. Its physiological role is likely to be in the remodelling of the bacterial sacculus during growth. Example (prepro precursor) from *Staphylococcus simulans*: database code LSTP_STASI, 389 amino acids (42.19 kDa). The C terminus has some similarity to **autolysin**.

lysozyme EC 3.2.1.17; *systematic name*: peptidoglycan *N*-acetylmuramoylhydrolase; *other name*: muramidase. An enzyme that hydrolyses β-1,4-linkages between *N*-acetylmuramic acid and 2-acetamido-2-deoxy-D-glucose residues in peptidoglycan heteropolymers (mucopolysaccharide or muropeptide) of prokaryote cell walls. It occurs in tears, other exocrine secretions, and in very large amounts in the white of eggs of birds. The antibacterial action of lysozyme depends on the cleavage of the $\beta(1\rightarrow4)$glycosidic linkage between alternating units of *N*-acetylmuramic acid and *N*-acetylglucosamine that form long-chain mucopolysaccharides in the cell walls of bacteria such as *Micrococcus luteus*. There are a number of types of lysozyme, designated A–G. They belong to the **lactalbumin/lysozyme family**. Example of egg-white lysozyme from *Gallus gallus* (domestic fowl): database code NRL_4LYM, 129 amino acids (14.30 kDa); 3-D structure known (first enzyme of which this was true).

[Lys^8]vasopressin *abbr. for* [8-lysine]vasopressin.

lysyl the acyl group, H_2N–$[CH_2]_4$–$CH(NH_2)$–CO–, derived from **lysine**.

lysylbradykinin *or* **Lys-bradykinin** *an alternative name for* kallidin; *see* **bradykinin**.

lysyl endopeptidase EC 3.4.21.50; *other names*: *Achromobacter* proteinase I; lysyl bond specific proteinase. An extracellular bacterial serine proteinase that preferentially cleaves at Lys-|-Xaa, including Lys-|-Pro.

lysyl oxidase EC 1.4.3.13; *recommended name*: protein-lysine 6-oxidase; *systematic name*: protein-L-lysine:oxygen 6-oxidoreductase (deaminating). An enzyme that catalyses a reaction between peptidyl-L-lysyl-peptide, H_2O and dioxygen to form peptidyl-allysyl-peptide, NH_3, and H_2O_2. Example (precursor) from human: database code LYOX_HUMAN, 417 amino acids (46.89 kDa). *See also* **allysine**.

+lyte *comb. form* indicating a substance that can be decomposed, broken down, or lysed.

lytic 1 of, pertaining to, or resulting from **lysis**. 2 of, or pertaining to a **lysin**.

+lytic *see* **+lysis**.

lyticase *a jargon term for* a combination of enzymes, with min-

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imal amounts of nucleases, that displays two major activities: β-1,3-glucanase and a highly specific alkaline protease. It is prepared from *Oerskovia xanthineolytica* and is useful in removing cell walls from yeasts and fungi, causing extremely rapid cell lysis.

lytic cycle the sequence of events occurring when a sensitive bacterium is infected by a virulent bacteriophage. The phage diverts the metabolism of the cell to the exclusive production of progeny phage, resulting in the lysis of the host cell with liberation of phage.

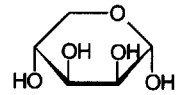
α-lytic endopeptidase EC 3.4.21.12; a bacterial serine proteinase, a homologue of chymotrypsin, that hydrolyses proteins, especially at bonds adjacent to L-Ala and L-Val residues in bacterial cell walls, elastin, and other proteins. Example from *Lysobacter enzymogenes*: database code NRL_2ALP, 198 amino acids (19.84 kDa); 3-D structure known.

lytic virus any virus including bacteriophages whose multiplication in a host cell leads to lysis of that cell.

Lyx *symbol for* a residue (or sometimes a molecule) of the aldopentose **lyxose**.

lyxo- *prefix (in chemical nomenclature)* indicating a particular configuration of a set of three (usually) contiguous >CHOH groups, as in the acyclic forms of D- or L-lyxose. *See* **monosaccharide**.

lyxose *symbol*: Lyx; *a trivial name for* the aldopentose, *lyxo*-pentose; the C-2 epimer of **xylose**, rare in nature.



α-D-lyxose (pyranose form)

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Mm

m *symbol for* **1** metre. **2** milli+ (SI prefix denoting 10^{-3} times).

m+ *prefix (in peptide hormone nomenclature)* denoting mouse, murine; derived, or as if derived, from a mouse.

m_r *symbol for* relative electrophoretic mobility.

m *symbol for* **1** mass; the various associated terms are distinguished by subscripts: m_e, *symbol for* electron rest mass; m_n, *symbol for* neutron rest mass; m_p, *symbol for* proton rest mass; m_u, *symbol for* atomic mass constant. **2** molality (alternative to *b*). **3** (bold italic) magnetic moment.

m- *prefix (in chemical nomenclature)* denoting ***meta-***. *Compare* ***o-***, ***p-***.

M *symbol for* **1** mega+ (SI prefix denoting 10^6 times). **2** a residue of the α-amino acid L-methionine (alternative to Met). **3** a residue of an incompletely specified base in a nucleic-acid sequence that may be either adenine or cytosine. **4** mesomeric effect. **5** a metal (in chemical formulae). **6** molar (concentration), i.e. moles per litre (alternative to M or *M*; mol dm^{-3} is recommended). **6** 6-mercaptopurine ribonucleoside, 6-thioinosine.

M *symbol for* molar (concentration), i.e. moles per litre (alternative to M or *M*; mol dm^{-3} is the recommended form).

α_2-M *abbr. for* α_2-macroglobulin.

M *symbol for* **1** mass, especially molar mass; related terms are designated by subscripts: M_m, *symbol for* mass-average molar mass (*see* **average molar mass**); M_n, *symbol for* number-average molar mass (*see* **average molar mass**); M_o, *symbol for* mean relative residue mass; M_r, *symbol for* relative molecular mass; M_w, symbol for weight-average molar mass; M_z *symbol for* Z-average molar mass (*see* **average molar mass**). **2** molar (concentration), i.e. moles per litre (alternative to M or M; no longer recommended; use mol dm^{-3}). **3** (*or* M_v) luminous exitance. **4** (*or* M_e) radiant exitance. **5** (bold italic) magnetization. **6** (bold italic) moment of a force.

MAA *abbr. for* macroaggregated (human serum) albumin.

MAC *abbr. for* **1** membrane attack complex. **MAC 1** is a cell-surface glycoprotein of monocytes, macrophages, and granulocytes that is implicated in adhesive interactions of these cells as well as in mediating the uptake of complement-coated particles. It probably recognizes the RGD peptide in **complement** component C3b. It is a heterodimer of α_M and β_2 chains (*see* **integrin**). Examples: (human) MAC 1 α_M (precursor): database code ITAM_HUMAN, 1153 amino acids (127.16 kDa); MAC 1 β_2 (precursor): database code ITB2_HUMAN, 769 amino acids (84.69 kDa). **2** mammalian artificial chromosome.

MACIF *abbr. for* membrane attack complex inhibition factor.

MAC-IP *abbr. for* MAC-inhibitory protein (i.e. **CD59**).

mackerel any marine fish of the subfamily Scombroidei. These fish are of importance as food fish, and their flesh is rich in oils with a relatively high content of *n*-3 **fatty acids**; typical composition (major fatty acids, expressed as percentage of total fatty acids): 14:0, 8%; 16:0, 16%; 18:0, 2%; 16:1 (*n*-7) 8%; 18:1 (*n*-9), 8%; 18:1 (*n*-7), 4%; 18:4 (*n*-3), 2%; 20:1 (*n*-9), 11%; 20:5 (*n*-3), 8%; 22:1 (*n*-11), 13%; 22:6 (*n*-3), 8%.

Macleod, John James Richard (1876–1935), British physiologist and biochemist; Nobel Laureate in Physiology or Medicine (1923) jointly with F. G. Banting 'for the discovery of insulin'.

maconha *see* **cannabis**.

macro+ *or (before a vowel)* **macr+** *comb. form* **1** denoting large, long, or great in size or duration; large-scale. **2** denoting larger than normal, overdeveloped. *Compare* **micro+**.

macroaggregate any macromolecular aggregate large enough to be visible to the unassisted eye.

macrocycle any **macrocyclic** compound.

macrocyclic **1** *(in chemistry)* describing any compound containing a ring structure consisting of a large number (usually 15 or more) atoms. **2** *(in biology)* having a long life cycle.

macrocytic anemia anemia in which the circulating erythrocytes are larger than normal. It is often due to deficiency of vitamin B_{12} (cobalamin) or folic acid.

macroglobulin any plasma globulin of >400 kDa. Macroglobulins include **immunoglobulin M**, **α_2-macroglobulin**, and many lipoproteins.

α_2-macroglobulin *abbr.*: α_2-M; a glycoprotein found in vertebrate plasma that strongly inhibits proteinases of all classes. In humans it constitutes about one third of the α_2-globulins; in hypoalbuminemia its synthesis is enhanced, when it constitutes a major proportion of the increased α_2-globulin band on electrophoresis strips. Human α_2-M is a 726 kDa molecule comprising two pairs of disulfide-linked, identical 185 kDa subunits, which also contain heterodetic peptide rings containing reactive thiol ester linkages, each formed between the γ-carboxyl group of a glutamic residue and the thiol group of a cysteine residue in the same peptide chain. It can inhibit all four classes of **proteinase** by a mechanism involving a **bait region**. This contains specific sites, cleavage of which induces a conformational change that results in trapping of the proteinase: following cleavage in the bait region a thiol-ester bond is hydrolysed and mediates the covalent binding of the protein to the proteinase; subsequently ε-amino groups of the proteinase react with the thiol-ester linkages in the inhibitor to form stable amide links. The entrapped proteinase is then able to act on substrates of low molar mass only. Example, subunit precursor from human: database code A2MG_HUMAN, 1474 amino acids (163.09 kDa).

macroglobulinemia *or (esp. Brit.)* **macroglobulinaemia** a condition in humans in which there is an increase in the concentration of macroglobulins, especially immunoglobulin M, in the blood. It is often associated with lymphocyte tumours.

macro histone 2A *abbr.*: macro H2Aa; the counterpart of histone H2A that replaces this in certain nucleosomes, with an implied role in nucleosome positioning. Example from rat: database code H2AM_RAT, 367 amino acids (38.91 kDa).

macroion an ion of a macromolecule, especially one that does not pass through a dialysis membrane.

macrolide any of a large group of structurally related antibiotics produced by *Streptomyces* spp. They contain a large lactone ring (*see* **+olide**) with few or no double bonds and no nitrogen atoms, linked glycosidically to one or more sugar moieties. The macrolides include the carbomycins, the **erythromycins**, oleandomycin, **oligomycins**, and the spiramycins. They are active mainly against Gram-positive bacteria and they inhibit the early stages of protein synthesis.

macroligand (*sometimes*) any macromolecular ligand.

macrometabolite (*sometimes*) any metabolite present in a system in reasonably high concentration, especially as opposed to a trace metabolite, i.e. one present in extremely small concentrations.

macromolecule any molecule composed of a very large number of atoms, operationally defined as any molecule of mass greater than about 10 kDa (and ranging up to 10^2 MDa or more) that is incapable of passing through the pores of dialysis tubing as generally used. The term includes nucleic acids and most polysaccharides and proteins. *Compare* **micromolecule**. —**macromolecular** *adj.*

macronutrient any element that is required by living organisms in relatively large quantities for normal growth. *Compare* **micronutrient**.

macrophage any cell of the **mononuclear phagocyte system** that is characterized by its ability to phagocytose foreign particulate and colloidal material. Macrophages occur in connective tissue, liver (Kupffer cells), lung, spleen, lymph nodes, and other tissues. They contain prominent lysosomes, stain with vital dyes, and play an important part in nonspecific immune reactions.

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macrophage-activating factor *abbr.*: MAF; *see* **lymphokine**.

macrophage-colony stimulating factor *see* **colony stimulating factor**.

macrophage inflammatory protein *abbr.*: MIP; any of a number of cytokines produced by B and T cells, monocytes, mast cells, and fibroblasts. MIP 1α is a chemoattractant for monocytes, T cells, and eosinophils; it also inhibits hematopoietic stem cell production; example from *Mus musculus*: database code MI1A_MOUSE, 92 amino acids (10.34 kDa); residues 1–23 are the signal peptide. MIP 1β is a chemoattractant for monocytes and T cells and is an adhesion molecule, binding to β_1 (**VLA** family) **integrins**; example from *M. musculus*: database code MI1B_MOUSE, 92 amino acids (10.17 kDa); residues 1–23 are the signal peptide.

macrophage migration enhancement factor *see* **lymphokine**.

macrophage migration inhibitory factor *abbr.*: MIF; *other name*: delayed early response protein 6; a **lymphokine** that is released by primed lymphocytes on incubation with the priming antigen. It inhibits the migration of macrophages out of macrophage-rich tissue such as spleen, and is probably a mediator of macrophage participation in inflammation. Example from human: database code MIF_HUMAN, 114 amino acids (12.30 kDa).

macrophage system *see* **mononuclear phagocyte system**.

macropipette (*sometimes*) a pipette of similar construction to a standard plunger-type micropipette but of capacity in the range 0.25–5 mL.

macropore any pore (in a gel or porous solid) whose width is greater than about 50 nm. *Compare* **mesopore**, **micropore**. —**macroporous** *adj.*

macroreticular describing a three-dimensional polymer with a very open structure, the cross links being widely spaced.

macroscopic **1** of a size that is visible to the unaided eye. *Compare* **microscopic** (def. 1). **2** concerned with large units. *Compare* **microscopic** (def. 2). **3** relating to the behaviour of atoms or molecules in bulk. *Compare* **microscopic** (def. 3). —**macroscopically** *adv.*

macroscopic equilibrium constant any constant describing the overall equilibrium between two chemical entities that may be interconverted through two or more alternative intermediates. *Compare* **microscopic equilibrium constant**.

macrosolute *an operational term describing* any solute of a size larger than will pass through a membrane of a specified pore size or permeability limit.

macrotetrolide *or* **macrotetralide** any of a group of antibiotics characterized structurally by the presence of a 32-membered ring built up of four hydroxy-acid residues and containing four ether and four ester bonds; the group includes **nonactin** and related antibiotics. Some similar compounds have an open-chain structure, e.g. **monensin** and **nigericin**.

macula adherens *an alternative term for* **desmosome**.

MadCAM *abbr. for* mucosal addressin cell adhesion molecule; MadCAM 1, M_r 58–66 kDa, is a member of the immunoglobulin superfamily of **adhesion molecules**. It is constitutively expressed on endothelial cells of post-capillary venules. It mediates lymphocyte homing to mucosal lymphoid organs and lamina propria venules, and binds L-**selectin** and **integrin** $\alpha_4\beta_7$. Example from *Mus musculus*: database code 533601, 405 amino acids (43.65 kDa).

mad cow disease *an informal name for* **bovine spongiform encephalopathy**.

madder the ground root of *Rubia tinctoria*, used as a plant dyestuff; the principal component is **ruberythric acid**.

MAF *abbr. for* macrophage-activating factor; *see* **lymphokine**.

magainin any of several antibiotic peptides from *Xenopus* skin, whose pore-forming activity (*see* **PFP**) results in the permeabilization of bacterial membranes. They have a wide spectrum of action against bacteria, protozoa, and fungi. Magainin I has the sequence

GIGKFLHSAGKFGKAFVGEIMKS;

magainin II is (Lys[10],Asn[22])-magainin I. An analogue with greater antibiotic potency is (Ala[8,13,18])-magainin II amide. *Compare* **dermaseptin**.

magic spot I *see* **magic spot (compound), ppGpp**.

magic spot II *see* **magic spot (compound), pppGpp**.

magic spot (compound) *abbr.*: MS; either of the guanosine polyphosphates produced when stringent strains of *Escherichia coli* are starved of an amino acid required for protein synthesis. MS I is guanosine 5′-diphosphate 2′-(or 3′)-diphosphate (*symbol*: ppGpp); MS II is guanosine 5′-triphosphate 2′-(or 3′)-diphosphate (*symbol*: pppGpp).

magnesium *symbol*: Mg; a metallic element – an alkaline earth metal – of group 2 of the IUPAC **periodic table**; atomic number 12; relative atomic mass 24.305. It occurs naturally only in the combined state and is a mixture of stable nuclides of mass 24, 25, and 26. Magnesium is one of the most abundant elements of the Earth's crust and an essential component of all living material. It forms a divalent cation, Mg^{2+}, which is a component of chlorophyll, occurs in bone, and is an essential cofactor for many enzymes, including the majority of enzymes utilizing ATP. It is a major biological cation, the fourth most abundant cation in the human, much of it being in the skeleton; the range in normal human plasma is 0.8–1.2 mmol L^{-1}. An excretion mechanism in the kidney is partly regulated by parathyroid hormone. *See also* **magnesium-28**.

magnesium-28 the artificial radioactive nuclide of magnesium, $^{28}_{12}Mg$, of half-life 21.2 h. It emits a moderate-energy beta particle (i.e. electron) (0.46 MeV max.) and gamma radiation of various energies (1.35, 0.95, 0.40, and 0031 MeV).

magnesium porphyrin *a general term for* **chlorophyll**.

magnet any body that can produce an appreciable **magnetic field** external to itself. Magnets may be either permanent or temporary. —**magnetic** *adj.*

magnetic circular dichroism spectroscopy **circular dichroism spectroscopy** in the presence of a magnetic field.

magnetic constant *symbol*: μ_0; *an alternative name for* **permeability of vacuum**.

magnetic dipole moment *symbol*: $\boldsymbol{m}$ or $\boldsymbol{\mu}$ (italic bold); a vector quantity indicating the strength of a magnet: the product of a magnet's dipole moment and the ambient **magnetic flux density** gives the torque on the magnet. The SI unit is the A m^2 (ampere square metre = joule per tesla (J T^{-1})).

magnetic field **1** a field of force existing in the neighbourhood of either a permanent magnet or a circuit carrying an electric current. Another magnet will experience a couple when placed in a magnetic field. **2** *an alternative name for* **magnetic field strength**.

magnetic field strength *or* **magnetic field** *or (formerly)* **magnetic intensity** *symbol*: $\boldsymbol{H}$ (italic bold); a vector quantity, the magnetizing force at any point in a medium. It is measured by a couple that would act on a small magnet of unit moment placed at that point with its axis at right angles to the direction of the magnetic field. It is the **magnetic flux density**, $\boldsymbol{B}$, divided by the **permeability**, μ; i.e. $\boldsymbol{H} = \boldsymbol{B}/\mu$. The SI derived unit $\boldsymbol{H}$ = A m^{-1}.

magnetic flux *symbol*: Φ; a measure of the total strength of a magnetic field, defined as the scalar product of the magnetic flux density and the area. The SI derived unit is the **weber**.

magnetic flux density *or* **magnetic induction** *symbol*: $\boldsymbol{B}$ (italic bold); a pseudovector quantity, the **magnetic flux** passing through unit area of a magnetic field orthogonal to the magnetic force. The SI derived unit is the **tesla**.

magnetic force the force exerted by a magnetic field on a magnetic pole or a moving electric charge. It may be either attractive or repulsive.

magnetic immunoassay *abbr.*: MAIA; a variant of **radioimmunoassay** in which the antibody is bound to a particulate, inert, magnetic support material – e.g. cellulose containing embedded grains of iron oxide, Fe_3O_4 – and separation of antigen–antibody complexes from free antigen is effected with the aid of a powerful magnet.

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magnetic induction *an alternative term for* **magnetic flux density**.

magnetic intensity *a former name for* **magnetic field strength**.

magnetic lens *an alternative name for* a magnetic **electron lens**.

magnetic moment **1** *symbol*: μ; a property of a charged particle arising from its spin; $\mu = eL/2mc$, where c is the velocity of light, L is the angular momentum of the particle, e is its charge, and m is its mass. The SI unit is joule per tesla. The **electron magnetic moment** (*symbol*: μ_e) is equal to $9.284\ 7701 \times 10^{-24}$ J T^{-1}. **The proton magnetic moment** (*symbol*: μ_p) is equal to $1.410\ 607\ 61 \times 10^{-26}$ J T^{-1}. **2** *an alternative name for* **magnetic dipole moment**.

magnetic permeability *see* **permeability, permeability of vacuum**.

magnetic pole either of the two regions of a magnet into which the lines of force of the magnetic field converge or from which they diverge. They are designated north (or north-seeking) and south (or south-seeking) according to whether they are attracted to the Earth's north or south pole.

magnetic resonance *see* **electron-spin resonance spectroscopy, nuclear magnetic resonance**.

magnetic resonance imaging *abbr.*: MRI; an imaging technique that uses **nuclear magnetic resonance** (NMR) to investigate the state of tissues in the intact body; it is so-called to avoid the use of the term 'nuclear' in the treatment of patients. It has the advantage that it is non-invasive. A magnet large enough to surround a part of the body is used in conjunction with computer analysis to provide an image resulting from the NMR signals. The technique can distinguish extracellular water from that inside cells; this distinction is used to reveal certain types of tissue damage.

magnetic resonance zeugmatography *see* **zeugmatography**.

magnetic shielding **1** protection from the effects of an external magnetic field. **2** (in **nuclear magnetic resonance spectroscopy**) the reduction of the applied magnetic field at an atomic nucleus (as compared with that applied to the whole sample) brought about by the electron cloud of the molecule.

magnetic stirrer any apparatus for stirring a liquid in which a follower – usually a small bar magnet coated in glass or plastic – may be caused to oscillate or rotate within the liquid under the influence of a more powerful magnet outside the container. Motion of the external magnet is controlled by a variable-speed electric motor. The term is sometimes applied specifically to the follower.

magnetic susceptibility *symbol*: X *or (sometimes)* X_m *or* K; the ratio of the magnetization, M, produced in a substance to the magnetic field strength, H, applied to it, i.e.

$$X = M/H = \mu_r - 1,$$

where μ_r is the relative permeability of a vacuum. Paramagnetic materials have positive magnetic susceptibilities, diamagnetic materials have negative magnetic susceptibilities. (Note: the symbol μ_m is reserved for molar magnetic susceptibility.)

magnetism **1** the property of producing, or being affected by, magnetic flux. **2** the branch of physics concerned with magnets and magnetic phenomena.

magnetite *or* **magnetic iron oxide** *or* **black iron oxide** ferrosoferric oxide; iron(II)–diiron(III) oxide; Fe_3O_4; a strongly magnetic black mineral form of iron oxide.

magnetization *or* **magnetisation** **1** the act or process of magnetizing. **2** *symbol*: M (italic bold); the magnetic moment per unit volume of a magnetized body; i.e. the difference between the ratio of the **magnetic flux** to the **permeability of vacuum** and the **magnetic field strength**. The SI unit is the ampere per metre.

magnetization-transfer nuclear magnetic resonance spectroscopy a procedure in **nuclear magnetic resonance spectroscopy** in which one of the resonances is saturated by a strong radiofrequency field, and the changes in the other resonances are observed. It is useful in measuring the rates of chemical exchange processes.

magnetize *or* **magnetise** to induce a magnetic flux density in (something); to cause (something) to exhibit **magnetism** (def. 1).

magnetogyric ratio *see* **gyromagnetic ratio**.

magneton a unit of magnetic moment. The **Bohr magneton** (*symbol*: μ_B) refers to an electron of mass m_e; the **nuclear magneton** (*symbol*: μ_N) refers to a proton of mass m_p. They are related by the equation: $\mu_N = (m_e/m_p)\mu_B$.

magnetophoresis the movement of magnetizable particles through a fluid under the action of a magnetic field. It is useful for separating of dispersed cells to which ferromagnetic microspheres have been conjugated. —**magnetophoretic** *adj.*

magnification *(in microscopy)* the apparent linear enlargement of an object when viewed through a lens, system of lenses (as in a microscope, telescope, etc.), or other instrument. It is given by the ratio of the apparent diameter of the object, as seen using the lens, to its real diameter, as seen unaided.

Magnogel *a proprietary name for* a bead-form support material useful in immunosorption and related procedures. It is similar to **Ultrogel** but contains embedded particles of iron oxide, Fe_3O_4, that enable the beads to be drawn to and held on the walls of the container by magnetism.

MAIA *abbr. for* magnetic immunoassay.

Maillard reaction a nonenzymic reaction in which a reducing sugar combines at its anomeric carbon atom with an amino group of an amino acid, peptide, or protein to form first a Schiff base and then, by an **Amadori rearrangement**, the corresponding ketoamine. The reaction is the initial step of a series that may occur during the processing and/or storage of food and that can result in a loss of nutritive value and the formation of a brown coloration; hence it is also known as the **browning reaction**. It may also be the reaction leading to the formation of hemoglobin A_{1c} in the erythrocyte. [After Louis Camille Maillard (1878–1936).]

major groove the larger and deeper of the two spiral grooves on the surface of a double-helical B-DNA molecule. *Compare* **minor groove**.

major histocompatibility complex *abbr.*: MHC; a complex of genetic loci occurring in higher vertebrates that encodes a family of cellular antigens, known in mice as **histocompatibility-2 antigens** (*abbr.*: H-2 antigens; *see* **histocompatability antigen**) and in humans as human leukocyte-associated antigens (*abbr.*: HLA antigens; *see* **HLA histocompatibility system**). The MHC antigens are cell-surface glycoproteins and may be divided into two classes, designated I and II. In transplantation reactions, cytotoxic T lymphocytes respond mainly against foreign MHC glycoproteins of class I together with antigen, while the response against class II and antigen is mainly by helper T lymphocytes.

Class I MHC antigens (*or* transplantation antigens) are glycoproteins found on the surface of most nucleated somatic cells that enable the immune system to distinguish self from foreign cells. They are encoded by three separate loci (H-2K, H2-D, and H-2L in mice; HLA-A, HLA-B, and HLA-C in humans). The antigenic activity resides in a single polypeptide chain, the α subunit, of ≈45 kDa (roughly 345 amino acids) inserted into the cell membrane with a short hydrophilic C-terminal segment inside the cell, a short hydrophobic segment traversing the membrane, and a large carbohydrate-containing N-terminal segment. This N-terminal segment is folded into three separate domains (two of which contain a single intrachain disulfide bond) and exposed to the cell exterior, where it is noncovalently linked with the β subunit, an 11.5 kDa molecule also called β_2 microglobulin, which is homologous with a single Ig-like domain (*see* **immunoglobulin fold**). In humans, these proteins are also referred to as **HLA class I**.

Class II MHC antigens are found on the surface of only certain cell types; these include most B lymphocytes, some T lymphocytes, and some macrophages and macrophage-like cells. They are encoded by murine I-region (*abbr.*: Ir) genes and human HLA-D genes, and are two-chain proteins having a ≈33 kDa α chain and a 28 kDa β chain; the C-terminal regions of both subunits (α and β) have transmembrane and intracellular domains. Celiac disease is due to an allelic variant in one

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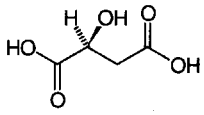
class-II gene. Example, α from human B-lymphoblastoid cell line: database code HUMMHDRARN, 229 amino acids (25.83 kDa); β-1 from human B-lymphocyte cell line: database code HUMMHDRBWB, 94 amino acids (11.40 kDa).

major tranquillizer *a term, now deprecated, for* any drug used to treat major psychosis, e.g. schizophrenia or mania; the term **neuroleptic** is now recommended.

MAK *abbr. for* methylated albumin-kieselguhr; a substance used as a medium for chromatography.

Mal **1** (when linked to one other group) *symbol for* the univalent maleyl group. **2** (when linked to two other groups) *symbol for* the bivalent maleoyl group.

malate **1** *a trivial name for* hydroxysuccinate; hydroxybutanedioate; $^{-}OOC–CH_2–CH(OH)–COO^{-}$; the dianion of malic acid, a chiral hydroxydicarboxylic acid. The (+)-enantiomer, (*S*)-malate (also designated L-malate), is an important intermediate in metabolism as a component of both the tricarboxylic-acid cycle and the glyoxylate cycle. **2** any mixture of free malic acid and its mono- and dianions. **3** any salt or ester of malic acid.



(*S*)-malate

malate–aspartate cycle *or* **malate cycle** an intracellular metabolic cycle, also known as the malate–aspartate shuttle or malate shuttle, that can transfer reducing equivalents from the cytoplasm to the mitochondria in liver and other tissues. Oxaloacetate formed inside the mitochondria is there converted by a transaminase into aspartate, which passes through the mitochondrial membrane on a specific carrier; a similar transaminase in the cytoplasm converts this aspartate back into oxaloacetate, which then reacts with cytoplasmic NADH, in a reaction catalysed by cytoplasmic **malate dehydrogenase**, to form (*S*)-malate and NAD^+. The malate thereupon passes back into the mitochondria, where it is dehydrogenated again to oxaloacetate, with concomitant reduction of mitochondrial NAD^+ to NADH and completion of the cycle.

malate dehydrogenase **1** *abbr.*: MDH *or (in clinical chemistry)* MD; EC 1.1.1.37; *recommended name*: malate dehydrogenase; *systematic name*: (*S*)-malate:NAD^+ oxidoreductase; *other name*: malic dehydrogenase. An important and widespread enzyme that interconverts malate and oxaloacetate according to the reaction:

(*S*)-malate + NAD^+ = oxaloacetate + NADH.

In yeast, e.g., there are three isoenzymes: cytoplasmic, glyoxysomal, and of the mitochondrial matrix. Example from yeast mitochondrial matrix, homodimer (precursor): database code MDHM_YEAST, 334 amino acids (35.53 kDa). **2** EC 1.1.1.82; *recommended name*: malate dehydrogenase ($NADP^+$); *systematic name*: (*S*)-malate:$NADP^+$ oxidoreductase. A chloroplast enzyme required for both C_3 and C_4 pathways (*see* **reductive pentose phosphate cycle**, **Hatch–Slack pathway**) to allow plants to circumvent the problem of photorespiration. It catalyses the reaction:

(*S*)-malate + $NADP^+$ = oxaloacetate + NADPH.

Example (precursor) from maize: database code MDHC_MAIZE, 432 amino acids (46.81 kDa). *See also* **malate dehydrogenase (decarboxylating)**.

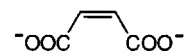
malate dehydrogenase (decarboxylating) any of several enzymes that bring about the oxidation of malate with simultaneous decarboxylation of the product to pyruvate. They include: (1) Malate dehydrogenase (oxaloacetate decarboxylating), EC 1.1.1.38; *systematic name*: (*S*)-malate:NAD^+ oxidoreductase (oxaloacetate decarboxylating); *other names*: malic enzyme; pyruvic–malic carboxylase; malate oxidoreductase; it catalyses the reversible reaction:

(*S*)-malate + NAD^+ = pyruvate + CO_2 + NADH.

Example, mitochondrial enzyme (a tetramer that can use $NADP^+$) from human (precursor): database code MAOM_HUMAN, 584 amino acids (65.37 kDa). (2) Malate dehydrogenase (decarboxylating), EC 1.1.1.39; *systematic name*: (*S*)-malate:NAD^+ oxidoreductase (decarboxylating); *other names*: malic enzyme; pyruvic–malic carboxylase; it catalyses a reaction between (*S*)-malate and NAD^+ to form pyruvate, CO_2, and NADH. (3) Malate dehydrogenase (oxaloacetate decarboxylating) ($NADP^+$), EC 1.1.1.40; *systematic name*: (*S*)-malate:$NADP^+$ oxidoreductase (oxaloacetate decarboxylating); *other names*: malic enzyme; pyruvic–malic carboxylase; it catalyses a reaction between (*S*)-malate and $NADP^+$ to form pyruvate, CO_2, and NADPH. It is an important enzyme in generating NADPH in the cytosol of mammals. Thus types 1 and 2 utilize NAD^+, while only types 1 and 3 decarboxylate added oxaloacetate, which leads to three activities being distinguished. (4) D-Malate dehydrogenase (decarboxylating), EC 1.1.1.83; *systematic name*: (*R*)-malate:NAD^+ oxidoreductase (decarboxylating); it catalyses a reaction between (*R*)-malate and NAD^+ to form pyruvate, CO_2, and NADH.

malate synthase EC 4.1.3.2; *systematic name*: L-malate glyoxylate-lyase (CoA-acetylating); *other names*: malate synthetase; malate condensing enzyme; glyoxylate transacetylase. An enzyme that catalyses the formation of L-malate and CoA from acetyl-CoA, H_2O, and glyoxylate. This is the second step in the glyoxylate bypass, an alternative to the complete tricarboxylic-acid cycle (in bacteria and plants). Example from *Escherichia coli*: database code MASY_ECOLI, 533 amino acids (60.21 kDa).

maleate **1** *the trivial name for cis*-1,2-ethylenedicarboxylate; (*Z*)-butenedioate; the dianion of maleic acid, the diastereoisomer of fumarate. **2** any mixture of maleic acid and its mono- and dianions. **3** any salt or ester of maleic acid.

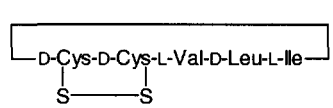


maleoyl *symbol*: Mal; the bivalent *cis*-acyl group, –CO–CH=CH–CO–, derived from maleic acid.

maleyl *symbol*: Mal; the univalent *cis*-acyl group, HOOC–CH=CH–CO–, derived from maleic acid.

maleylation the introduction of one or more **maleyl** groups into a substance by acylation, e.g. with maleic anhydride. Maleylation of a protein with maleic anhydride is used to acylate its free lysine (and other) amino groups in order to change their charge at neutral pH from positive to negative and to render the adjacent peptide bonds resistant to hydrolysis by trypsin; it can also lead to disaggregation of a multimeric protein. The reaction occurs at pH 8.5 (usually at 2 °C) and the maleyl groups can be removed at pH 3.5 (usually at 60 °C). Maleylation of thiol groups may also occur. *Compare* **citraconylation**, **succinylation**. **—maleylate** *vb.*

malformin A a cyclic pentapeptide from *Aspergillus niger* that causes curvature and malformations of various plants. The structure contains D-enantiomers of cysteine and leucine.



malic enzyme *or* **pyruvic–malic carboxylase** *a trivial name commonly applied to* any of three enzymes, found in most organisms, that catalyse the oxidative decarboxylation of (*S*)-malate with concomitant production of pyruvate. *See* **malate dehydrogenase (decarboxylating)**.

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malignant *(in pathology)* **1** (of a tumour) invasive, spreading, resistant to therapy. **2** (of a disorder) becoming progressively more serious if not treated.

malnutrition any imbalance, usually a deficiency, between the nutrients taken in by an organism and the amounts necessary to maintain that organism's normal development and health.

malonate **1** *the trivial name for* propanedioate; methanedicarboxylate; $^{-}OOC–CH_2–COO^{-}$, the dianion of malonic acid. It is a potent competitive inhibitor of **succinate dehydrogenase**. **2** any mixture of free malonic acid and its mono- and dianions. **3** any salt or ester of malonic acid.

malonate semialdehyde *the recommended trivial name for* malonate semialdehyde; formylethanoate; $OHC–CH_2–COO^{-}$. It is an intermediate in the oxidation of propionyl-CoA to acetyl-CoA in the terminal stages of the beta oxidation of fatty acids with an odd number of carbon atoms in plants.

malonyl **1** *(in biochemistry)* the univalent acyl group, $HOOC–CH_2–CO–$, derived from malonic acid by loss of one hydroxyl group. **2** *(in chemistry)* the bivalent acyl group, $–CO–CH_2–CO–$, derived from malonic acid by loss of both hydroxyl groups.

malonyl-CoA a key intermediate in fatty-acid biosynthesis, formed by reaction of carbon dioxide with acetyl-CoA, with hydrolysis of ATP to ADP and inorganic phosphate. This is catalysed by **acetyl-CoA carboxylase**; biotin is an essential cofactor. The plant enzyme also carboxylates propanoyl-CoA and butanoyl-CoA.

malonyl-CoA–acyl carrier protein transacylase EC 2.3.1.39; *recommended name*: [acyl-carrier-protein] *S*-malonyltransferase; *systematic name*: malonyl-CoA:[acyl-carrier-protein] *S*-malonyltransferase. An enzyme that catalyses a reaction between malonyl-CoA and ACP to form CoA and malonyl-ACP. It is a component of fatty-acid synthase in bacteria (*see* **fatty-acid synthase complex**). Example from *Escherichia coli*: database code FABD_ECOLI, 308 amino acids (32.25 kDa).

maloyl the bivalent acyl group, $–OC–CH(OH)–CH_2–CO–$, derived from malic acid by loss of the hydroxyl groups from both of its carboxyl groups.

Malpighian body *or* **Malpighian corpuscle** *or* **renal corpuscle** the part of a nephron comprising a cluster of blood capillaries (i.e. the renal glomerulus) together with the enclosing **Bowman's capsule**. [After Marcello Malpighi (1628–1694), Italian anatomist.]

malt **1** barley or other cereal grain that has been soaked in water, allowed to germinate, and then dried. In this process the starch of the cereal is largely degraded to maltose and other oligosaccharides. **2** to make into or become malt; to make or treat (something) with malt or an extract of malt.

maltase *a trivial name for* α-glucosidase; *see* **glucosidase** (def. 2).

malto- *comb. form (in chemical nomenclature)* designating an oligosaccharide or polysaccharide (e.g. maltose, maltotriose, maltoheptaose) consisting of D-glucopyranose residues in (α1→4)-linkage (as in maltose).

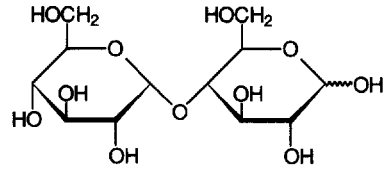
maltoporin a bacterial outer membrane transmembrane protein, with possibly 16 helices, having two roles in *Escherichia coli*: it transports maltodextrins (including maltose) into the cell, and acts as a receptor for lambda and some other phages. Example from *E. coli*: database code LAMB_ECOLI, 446 amino acids (48.86 kDa).

maltose *or (formerly)* **malt sugar** *the trivial name for* the disaccharide 4-*O*-α-D-glucopyranosyl-D-glucopyranose. It is an intermediate in the enzymic breakdown of glycogen and starch. (Illustrated top right.)

maltotriose the trisaccharide Glc(α1-4)Glc(α1-4)Glc; it is formed by the action of α-amylase on starch.

malt sugar *a former name for* **maltose**.

malyl either of the isomeric univalent acyl groups, $HOOC–CH(OH)–CH_2–CO–$ or $HOOC–CH_2–CH(OH)–CO–$, derived from malic acid by loss of a hydroxyl group from one or the other of the carboxyl groups.



maltose

mamma (*pl.* **mammae**) a mammary gland. —**mammary** *adj.*

mammal any animal of the Mammalia, a large class of warm-blooded tetrapod vertebrates characterized by the possession of sweat glands in the skin and, generally, an insulating layer of hair. Female mammals characteristically suckle their young at modified sweat glands – mammary glands – that secrete milk. Like birds, mammals possess a four-chambered heart, but their thoracic diaphragm is a uniquely mammalian feature. —**mammalian** *adj.*

mammalian artificial chromosome *abbr.*: MAC; a still hypothetical mammalian counterpart of a **yeast artificial chromosome** (YAC).

mammary gland *or* **mamma** the milk-secreting organ of a mature female mammal. The mammary glands occur in one or more pairs on the ventral surface.

mammotropic *or* **mammotrophic** *an alternative term for* **lactotropic**.

mammotropic hormone *or* **mammotrophic hormone** *an older name for* **prolactin**.

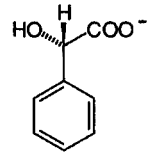
mammotropin *or* **mammotrophin** *an older name for* **prolactin**.

Man *symbol for* a residue (or a molecule) of the aldohexose mannose. In the condensed system of symbolism of sugar residues it signifies specifically a mannose residue with the common configuration and ring size, i.e. D-mannopyranose.

manaoic acid *see* **cyclic fatty acid**.

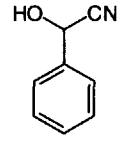
Mancini technique *see* **single radial immunodiffusion**.

mandelate α-hydroxybenzeneacetate; the anion, $C_6H_5–CH(OH)–COO^{-}$, derived from mandelic acid, the α-carbon atom of which is chiral. **2** any salt or carboxylic ester of mandelic acid.



L-(*S*)-(+)-form

mandelonitrile α-hydroxybenzeneacetonitrile; benzaldehyde cyanohydrin; a compound that occurs free and as β-glucosides of (+)-, (–)-, and (±)-mandelonitrile.



manganese *symbol*: Mn; a ferromagnetic, metallic transition element of group 7 of the IUPAC **periodic table**; atomic number 25; relative atomic mass 54.938. There is one stable nuclide of mass number 55. Manganese is widely distributed and abun-

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dant in the Earth's crust and is an essential component of all living material. It forms manganese(II) (manganous) and less stable manganese(III) (manganic) compounds, including ionic compounds, and complexes; it can also exist in higher oxidation states. Mn^{2+} ions act as activators of various enzymes. A number of artificial radioactive isotopes are known.

manifold a vessel or tube with a number of inlets or outlets used to collect or distribute gases or liquids in an apparatus.

manna a sweet-tasting, white to yellow dried exudate of the manna ash tree (*Fraxinus ornus*) and other plants. *See also* **manninotriose**.

mannan the main **hemicellulose** of soft (coniferous) wood, made up of D-mannose, D-glucose, and D-galactose in the ratio of 3:1:1. Glucomannans occur in ferns and others occur in certain higher plants and algae where they may function as the main structural component of the cell wall. Highly branched mannans can be extracted from the cell walls of some yeasts.

mannanase *or* **mannase** *see* **mannosidase** (def. 2).

Mannich reaction any chemical reaction in which an iminium ion of the type $CR'_2{=}N^+R_2$ reacts with a nucleophilic carbon atom, such as that of an enolate anion derived from a ketone or that of an activated double bond as in a phenol, aryl ether, pyrrole, or indole. Mannich reactions are believed to occur widely in biosynthetic pathways of polycyclic compounds, especially alkaloids and porphyrins. [After Carl Mannich (1877–1947).]

manninotriose the trisaccharide Gal(α1-6)Gal(α1-6)Glc; a component of **stachyose**, it also occurs free in **manna** from ash trees.

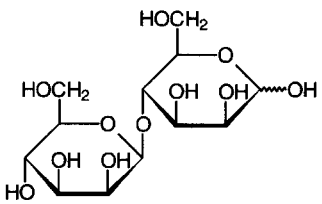
mannite *a former name for* **mannitol** (use deprecated).

D-mannitol the alditol derived from D-mannose by reduction of the –CHO group. It is widespread in higher plants, plant exudates, and algae, and is obtained from the manna ash (*Fraxinus ornus*) and seaweeds. Mannitol is metabolized by a number of bacteria including many strains of *Escherichia coli* and *Salmonella* spp. Clinically it is administered intravenously as an osmotic diuretic.

manno+ *comb. form* of mannose.

manno- *prefix (in chemical nomenclature)* indicating a particular configuration of a set of (usually) four contiguous >CHOH groups, as in the acyclic forms of D- or L-mannose. *See* **monosaccharide**.

mannobiose the disaccharide Man(β1-4)Man; a constituent of D-gluco-D-mannans isolated from hardwoods, and of polysaccharides from iris, orchid, and lily families.



mannoheptulose *manno*-2-heptulose; the D enantiomer (formerly known as D-*manno*-ketoheptose) occurs in the avocado.

mannokinase EC 2.7.1.7; an enzyme that catalyses the phosphorylation by ATP of D-mannose to D-mannose 6-phosphate with release of ADP. It initiates the further metabolism of mannose, e.g. after uptake by bacteria. Hexokinase has a wide specificity for sugars and catalyses this reaction, e.g., in mammalian liver.

mannosamine *symbol*: ManN; *a trivial name for* 2-amino-2-deoxymannose.

mannose *symbol*: Man; *a trivial name for* the aldohexose *manno*-hexose, the C-2 epimer of **glucose**. The D-(+)-form is widely distributed in mannans and hemicelluloses and is of major importance in the core oligosaccharide of N-linked oligosaccharides of glycoproteins, especially at branch points. A commonly occurring structure is Man(α1-6)[Man(α1-3)]-Man(β1-4)GlcNAc(β1-4)GlcNAc-Asn.

mannose 6-phosphate an intermediate in **mannose** metabolism, formed from mannose by **mannokinase** or from fructose 6-phosphate by **mannose-6-phosphate isomerase**. Apart from acting as a precursor in GDPmannose formation, it is a component of lysosomal enzymes, playing an important role in sorting the enzymes into lysosomes. *See also* **I-cell disease**, **mannose 6-phosphate receptor**.

mannose-1-phosphate guanylyltransferase EC 2.7.7.13; *other name*: GTP–mannose-1-phosphate guanylyltransferase; an enzyme that catalyses the reaction between GTP and α-D-mannose 1-phosphate to form GDPmannose with release of pyrophosphate. Example (fragment) from pig: database code A47415, 23 amino acids (2.49 kDa).

mannose-1-phosphate guanylyltransferase (GDP) EC 2.7.7.22; *systematic name*: GDP:D-mannose-1-phosphate guanylyltransferase. An enzyme involved in M-antigen biosynthesis in salmonellae; it catalyses a reaction between GDP and D-mannose 1-phosphate to form orthophosphate and GDPmannose. Example from *Salmonella choleraesuis*: database code CPSB_SALCH, 471 amino acids (52.57 kDa). This protein belongs to the **mannose-6-phosphate isomerase** family 2.

mannose-6-phosphate isomerase EC 5.3.1.8; *systematic name*: D-mannose-6-phosphate ketol-isomerase; *other names*: phosphomannose isomerase; phosphohexoisomerase; phosphohexomutase. An enzyme that catalyses the reaction:

D-mannose 6-phosphate = D-fructose 6-phosphate;

zinc is a cofactor. The sequences belong to two families. Example (family 1) from *Escherichia coli*: database code MANA_ECOLI, 391 amino acids (42.80 kDa). Most enzymes (including human) belong to this family. Family 2 is represented by an enzyme involved in alginate metabolism; example from *Pseudomonas aeruginosa*: database code ALGC_PSEAE, 462 amino acids (50.23 kDa). *See also* **mannose-1-phosphate guanylyltransferase**.

mannose 6-phosphate receptor a protein on the surface of membranes in the Golgi apparatus and late endosomes that recognizes mannose 6-phosphate residues on lysosomal enzymes and is responsible for sorting them into late endosomes, which then become lysosomes. Lysosomal enzymes bearing phosphomannosyl residues bind specifically to mannose-6-phosphate receptors in the Golgi apparatus, and the resulting receptor–ligand complex is transported to an acidic prelysosomal compartment where the low pH mediates dissociation. There are two types of receptor protein (examples are bovine): (1) the cation-dependent type – these are type I membrane glycoprotein dimers involved in transport of phosphorylated lysosomal enzymes from the Golgi apparatus and the cell surface to lysosomes; example (precursor): database code MPRD_BOVIN, 279 amino acids (31.17 kDa); (2) the cation-independent type – these are similar in action and with some sequence homology to the first type; example (precursor): database code MPRI_BOVIN, 2499 amino acids (274.22 kDa). *See also* **I-cell disease**.

mannosidase **1** α-mannosidase; EC 3.2.1.24; *systematic name*: α-D-mannoside mannohydrolase; an enzyme that catalyses hydrolytic removal of terminal, nonreducing residues in α-D-mannosides. Example from *Saccharomyces cerevisiae*: database code MAN1_YEAST, 1083 amino acids (124.5 kDa). **2** β-mannosidase EC 3.2.1.25; *systematic name*: β-D-mannoside mannohydrolase; *other names*: mannanase; mannase; an enzyme that catalyses hydrolytic removal of terminal, nonreducing residues in β-D-mannosides. Example from *Bos taurus*: database code A5881, 879 amino acids (101.06 kDa). *See also* **ER mannosidase**, **Golgi mannosidase**.

mannoside any **glycoside** in which the sugar moiety is a **mannose** residue.

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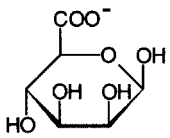
mannosyl any of the glycosyl ligands formed by detaching the anomeric (α- or β-) hydroxyl group, on C-1, from a cyclic form (pyranose or furanose) of mannose.

α-1,3-mannosyl-glycoprotein β-1,2-*N*-acetylglucosaminyltransferase EC 2.4.1.101; *other name*: *N*-glycosyl-oligosaccharide-glycoprotein*N*-acetylglucosaminyltransferase I (*abbr.*: GlcNAc-TI *or* GNT-I); an enzyme involved in the synthesis of oligosaccharides, particularly those that are N-linked in glycoproteins. It catalyses the reaction between UDP-*N*-acetyl-D-glucosamine and α-D-mannosyl-1,3-(R)-β-D-mannosyl-R′ to form *N*-acetyl-β-D-glucosaminyl-1,2-α-D-mannosyl-1,3-(R)-β-D-mannosyl-R′ with release of UDP. Example from human: database code GNT1_HUMAN, 445 amino acids (50.80 kDa).

mannuronate **1** the anion of mannuronic acid, the compound formed by oxidation of the C-6 hydroxymethylene group of mannose to a carboxyl group. **2** any salt or ester of mannuronic acid. D-Mannuronic acid is a component of **alginic acid**.



β-D-pyranose form

manoalide a naturally occurring marine sesterterpenoid. It is an irreversible inhibitor of phospholipases A_2 and C, and a potent inhibitor of Ca^{2+} mobilization.

manometer an instrument for measuring pressure differences. The simplest type consists of a U-tube filled with a suitable liquid (often mercury), and compares a pressure delivered to one side with atmospheric pressure on the other, open, side of the tube. The difference in the level of liquid in the two arms of the tube gives a measure of the unknown pressure. In biochemistry the term is often used to mean a manometric **respirometer**.

manometer constant a predetermined factor, calculated for each individual constant-volume manometric **respirometer**, that when multipled by the manometer reading immediately gives the volume of gas evolved in cubic millimetres at **standard** temperature and pressure. The factor is itself dependent upon temperature, liquid volume, density of the manometer fluid, and nature of the gas phase.

manometer fluid any fluid used to fill a **manometer**. In biochemistry this usually refers to the fluid used to fill the manometer of a respirometer. Such fluids are generally easily visible, wet the glass walls of the manometer, have a density that will give an easily calculated manometer constant, and have a low vapour pressure. Examples include **Brodie's fluid**, and **Krebs' manometer fluid**.

manometric **1** of, pertaining to, or measured with a **manometer**. **2** *(in biochemistry)* of, or pertaining to, a manometric respirometer. —**manometrically** *adv.*

manometry **1** the measurement of gas pressure by means of a manometer. **2** *(in biochemistry)* the use of manometric respirometers in studies of chemical and biochemical reactions.

Manp *symbol for* a mannopyranose residue.

mantissa the fractional part of any **logarithm**.

MAO *abbr. for* monoamine oxidase.

MAO inhibitor *abbr. for* monoamine oxidase inhibitor.

map **1** any representation of the surface features of an object, especially the spatial relationships of physical or chemical landmarks, as in **electron-density map**, **genetic map**, and **restriction map**. By extension the term is applied to certain two-dimensional patterns obtained in analysis, e.g. **peptide map**. **2** to make a **map** (def. 1). **3** to occur, or be placed, at a specific position on a **map** (def. 1).

MAP *abbr. for* microtubule-associated protein.

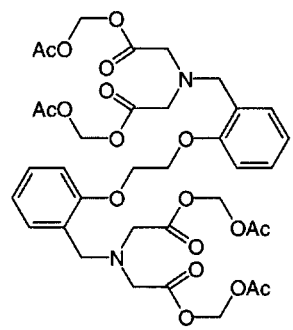
map distance *(in genetics)* the distance, in terms of percentages of crossing-over (i.e. 100 × no. of recombinants/total no. of progeny), between particular linked genes. *See also* **map unit**.

MAP kinase *abbr. for* mitogen-activated protein kinase; a family of protein kinases that perform a crucial step in relaying signals from the plasma membrane to the nucleus. They are turned on by a wide range of proliferation- or differentiation-inducing signals. Example, MAP kinase FUS3 of *Saccharomyces cerevisiae*, required for the transition from mitosis into conjugation: database code FUS3_YEAST, 353 amino acids (40.77 kDa). The name does not indicate that this is a kinase for MAPs – rather that it is a protein kinase that is mitogen-activated. Nevertheless, some MAPs can be substrates for this enzyme. *See also* **ERK**.

MAP kinase kinase *abbr.*: MAPKK; EC 2.7.1.–; a dual-specificity mitogen-activated protein kinase kinase; *other names*: ERK activator kinase; extracellular signal-regulated kinase; an enzyme that catalyses the concomitant phosphorylation of threonine (T) and tyrosine (Y) residues in a TEY sequence in **MAP kinases**. It requires activation by the serine/threonine kinase, MAP kinase kinase kinase (*see* ***RAF***). Examples from human: MAPKK 1, database code MPK1_HUMAN, 392 amino acids (43.28 kDa); MAPKK 2, database code MPK2_HUMAN, 400 amino acids (44.37 kDa).

maple-syrup urine disease *or* **branched-chain ketonuria** an autosomal recessive disease of humans characterized by neurological signs and the onset of feeding problems in the first week of life, and associated with a maple-syrup odour of the urine. The concentrations of branched-chain amino acids and branched-chain keto acids are elevated in the blood of patients, due to deficiency of the enzyme responsible for the oxidative decarboxylation of branched-chain keto acids.

MAPTAM 1,2-bis-(2-amino-5-methylphenoxy)ethane-*N,N,N′,N′*-tetraacetic acid tetraacetoxymethyl ester; a substance that readily penetrates cell membranes and undergoes intracellular hydrolysis with the formation intracellularly of the 5-methyl form of **BAPTA**. It is useful as an indicator of intracellular calcium concentrations.



map unit *or* **Morgan's unit** a unit of genetic length along a chromosome and defined in terms of recombination frequency, expressed as a percentage; a recombination frequency of 1 per cent (that is one recombinant individual in a hundred progeny) equals one map unit. 1 map unit = 1 centimorgan. *Compare* **morgan**.

marasmus a wasting away of the body, especially of infants, caused by chronic deficiency of intake of energy-producing foodstuffs. *Compare* **kwashiorkor**.

marcks *abbr. for* myristoylated alanine-rich C kinase substrate; a filamentous (F) actin cross-linking protein and the most prominent substrate for protein kinase C. It also binds

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calmodulin, actin, and synapsin and is displaced from the membrane by phosphorylation by protein kinase C. Example from human: database code MACS_HUMAN, 331 amino acids (31.38 kDa).

margarine a processed fat used as a substitute for butter. Modern margarines are prepared from hydrogenated natural fats, the trend in recent years having been to preserve a high content of nutritionally desirable **polyunsaturated fatty acids**. Apart from the oil or fat content, margarine contains a water phase that is 16–20% of content and includes water, cream, whole milk, skim milk (powder), whey, and buttermilk in various ratios; flavouring, which may include diacetyl, fatty acids, and ketones; colouring agents, mainly based on carotenes; additional vitamins A and D; and **antioxidants** such as di-*tert*-butyl *p*-cresol. The process was invented in 1869 by H. Mège-Mouriès on the order of Napoleon III to produce a cheap stable butter substitute. Mège-Mouriès churned a beef tallow fraction, known as **oleomargarine**, with cream.

marijuana *see* **cannabis**.

Mariotte bottle *or* **Mariotte flask** a device for providing a flow of liquid maintained at a constant pressure head; it is used, e.g., in column chromatography. It consists of a sealed flask, closed to the atmosphere, with an outlet at or near the bottom and an air inlet tube open to the atmosphere. The height of the bottom of the inlet tube is adjustable. When the flask is filled with liquid to a level above the bottom of the inlet tube the pressure of the liquid flowing from the flask is determined by the height of the bottom of the inlet tube above the outlet point. [After Abbé Edmé Mariotte (1620–84), French physicist.]

Mariotte's law *an alternative name (esp. Fr.) for* Boyle's law (*see* **gas laws**).

marker **1** an appropriate reference substance or material included in a sample being subjected to a separation procedure such as chromatography, electrophoresis, or density-gradient centrifugation. **2** *see* **biochemical marker**. **3** *see* **genetic marker**. **4** *an alternative term for* **label** (def. 3).

marker enzyme any enzyme of known intracellular location that can be assayed as an aid in following the isolation and purification of subcellular fractions.

marker gene any gene of known function and known location on a chromosome. *Compare* **genetic marker**.

marker rescue a process whereby one or more genetic markers from a UV-irradiated virus are integrated into an unirradiated helper virus in infected bacteria; such genes are thereby 'rescued' by recombination.

Markham still a simple, all-glass, steam-jacketed apparatus for the rapid and efficient steam distillation of a succession of small samples of volatile substances. It was designed especially for the distillation of ammonia as part of the micro-Kjeldahl procedure for the determination of nitrogen, but has been found to be prone to carry-over from one sample to the next. [After Roy Markham (1916–79), British biochemist.]

Markovnikov('s) rule a generalization stating that when a molecule of water, or a hydrogen halide, or some other polar substance, is added heterolytically across an asymmetrically substituted carbon–carbon multiple bond, the hydrogen atom or other more electropositive part of the molecule becomes attached usually to that carbon atom carrying the larger number of hydrogen atoms while the hydroxyl, halo, or other more electronegative part of the molecule becomes attached to that carbon atom carrying the smaller number of hydrogen atoms. [After Vladimir Vasilyevich Markovnikov (1838–1904), Russian chemist, who formulated the rule on empirical grounds (1870).]

Maroteaux–Lamy syndrome *an alternative name for* **mucopolysaccharidosis VI**.

marsh gas *another name for* **methane**.

Martin, Archer John Porter (1910–), British biochemist, physical chemist, and inventor; Nobel Laureate in Chemistry (1952) jointly with R. L. M. Synge 'for their invention of partition chromatography'.

MAS a human transforming gene that encodes a neuronal-type angiotensin III receptor. This is a transmembrane cell surface protein, mediating a G-protein-linked phosphoinositide response. Example: database code MAS_HUMAN, 325 amino acids (37.42 kDa).

maser a device for producing intense beams of microwave radiation of defined frequency. *Compare* **laser**. [From microwave amplification by stimulated emission of radiation.]

masked residue any residue in a biopolymer that is not accessible to, and cannot react with, a reagent specific for that type of residue, either because of the position of the residue or because of the nature of its immediate environment.

maspin a **serpin**-like tumour suppressor of epithelial cells. Example from human: database code HSU04313, 375 amino acids (42.09 kDa).

mass **1** *symbol: m* or *M*; one of the seven SI base physical quantities; the SI base unit of mass is the **kilogram**. **2** *a general term for* the quantity of matter in a body, a characteristic that is both a measure of the resistance of the body to changes in its velocity, i.e. **inertial mass**, and a measure of the force experienced by the body in a gravitational field, i.e. **gravitational mass**. Mass is commonly confused with weight. According to the theory of relativity, inertial and gravitational masses are equal, mass increases with velocity, and mass and energy are interconvertible.

mass action, law of a law stating that, for a homogeneous system, the rate of reaction of a chemical reaction is proportional to the active masses of the reacting substances; i.e. the rate is proportional to the product of the activities of the reactants, each raised to a power equal to the number of reactant molecules of that type that participate in the reaction.

mass-average molar mass *see* **average molar mass**.

mass concentration *see* **concentration** (def. 1a).

mass density *see* **concentration** (def. 1a).

mass fraction *symbol: w*; the mass of a specified component of a system divided by the mass of the system; it is dimensionless.

mass fragmentography *a common but less rigorous name for* **selected-ion monitoring**.

mass number *an older name for* **nucleon number**.

mass spec. *abbr. (colloquial) for* mass spectrometer, mass-spectrometric, or mass spectrometry.

mass spectrograph a **mass spectrometer** in which the ions fall on a photographic plate.

mass spectrometer *abbr.*: MS *or (colloquial)* mass spec.; any instrument for **mass spectrometry**.

mass spectrometry *abbr.*: MS *or (colloquial)* mass spec.; an analytical method for determining the relative masses and relative abundances of components of a beam of ionized molecules or molecular fragments produced from a sample in a high vacuum. It is applicable to any sample that is gaseous or volatile at low pressure, or that can be so rendered by derivatization. In the commonest version, the ions, generated usually by electron bombardment of the sample, are formed into a beam and then accelerated to a uniform velocity by means of an arrangement of electrically charged slits. The beam is then dispersed into a spectrum of particles of different mass-to-charge ratios, *m/e*, by application of a suitably disposed magnetic field. The ions of any particular *m/e* value may be focused on a collecting electrode by appropriate adjustment of the accelerating potential or magnetic field and the resulting ion currents measured electrometrically. With a suitably designed mass spectrometer the method can be used to determine the relative abundances of isotopes of an element or the relative molecular masses of two or more compounds, or used to aid the identification of a complex compound by the mass spectrum of the fragments generated from it on electron bombardment. *See also* **gas chromatography/mass spectrometry**, **selected-ion monitoring**. —**mass-spectrometric** *adj.*

mass spectrum a tracing, photographic record, or diagram of the relative numbers of different ions (representing molecules or molecular fragments) obtained (from a specimen) by

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mass spectrometry, ranked in order of their mass-to-charge ratios.

mass-to-charge ratio *(in mass spectrometry)* the ratio of the mass, *m*, of an ion to the charge, *e*, on the ion. *See also* **mass spectrometry**.

mass transfer the spontaneous and irreversible process of transfer of mass across nonhomogeneous fields, e.g. between liquid phases, or from one side of a membrane to another.

mass unit *see* **atomic mass unit**, **dalton**.

mast cell a type of leukocyte, of the subclass granulocyte; it is characterized by having numerous basophilic granules in the cytoplasm; these granules contain relatively large amounts of histamine together with 5-hydroxytryptamine and heparin. Degranulation of mast cells, with concomitant release of the vasoactive amines, occurs by reaction, through a specialized region of the Fc piece, of antigen with homocytotropic antibody (reagin) bound to the cell. This leads to an immediate hypersensitivity reaction.

mast cell degranulating peptide *abbr.*: MCDP; one of the major neurotoxic peptides of bee venom; the 22-residue peptide IKCNCKRHVIKPHICRKICGKN–NH_2. It stimulates degranulation of mast cells, and also selectively blocks the neuronal Ca^{2+}-dependent K^+ channel.

mast cell growth factor *see* **stem cell factor**.

mastoparan a tetradecapeptide toxin from wasp venom: Ile-Asn-Leu-Lys-Ala-Leu-Ala-Ala-Leu-Ala-Lys-Lys-Ile-Leu-NH_2. It is neurotoxic, and functions in a similar way to **melittin** and **mast cell degranulating peptide**, in generating ion channels in membranes.

MATα2 yeast mating-type protein α-2 repressor; a regulatory DNA-binding protein whose DNA recognition sequence (CATGTAATT) resembles a homeobox, the recognition sequence of homeobox proteins in higher organisms. MATα2 acts as a master switch in yeast differentiation by controlling gene expression in a cell-type-specific fashion. In α haploids and **a**/α diploids (*see* **mating type**) it represses the transcription of α-cell-specific genes. In **a**/α diploids it also forms a complex with MATα1 protein that represses haploid-specific gene expression. Database code MAT2_YEAST, 210 amino acids (24.25 kDa).

matchmaker proteins *see* **molecular matchmakers**.

maternal-effect gene a gene that is transcribed from the maternal genome during oogenesis, and expresses products at or immediately before fertilization, so that the phenotype of the embryo is determined by the maternal alleles alone. Genes that determine egg polarity, e.g. **oskar** are of this type.

mathematics **1** *functioning as sing.* the group of related sciences concerned with number, space, shape, and quantity, and their interrelationships. **2** *functioning as sing. or pl.* the use of mathematical processes or operations in calculations or the solution of problems.

mating type one of the two types of *Saccharomyces cerevisiae*, α and **a**, each of which is necessary for the occurrence of mating, a process in which two haploid cells fuse. The resulting diploid cell, **a**/α, cannot mate, but can produce spores, giving rise to haploid cells by meiosis. The mating type of the haploid cell is determined by a single locus, the mating-type (*MAT*) locus. In **a** cells, this encodes a single gene regulatory protein **a**1, and in an α cell it encodes two such proteins, α1 and α2. In the **a**/α cell, the regulatory proteins **a**1 and α2 combine to generate a completely new pattern of gene expression. *See also* **MATα2**.

matrilysin EC 3.4.24.23; *other names*: matrin; uterine metalloendopeptidase; matrix metalloproteinase 7 (*abbr.*: MMP7); putative (or punctuated) metalloproteinase-1 (*abbr.*: PUMP-1); an enzyme that catalyses the cleavage of Ala^{14}-|-Leu^{15} and Tyr^{16}-|-Leu^{17} in the B chain of insulin. It has no action on collagen types I, II, IV, or V. It cleaves casein and fibronectin and shows preference for gelatin chain α-2(I) over α-1(I). It is secreted as the precursor, promatrilysin, and is activated by autocatalytic cleavage at Glu^{77}-|-Tyr^{78}. Zinc and calcium are cofactors. Example (precursor) from human uterus: database code COG7_HUMAN, 267 amino acids (29.64 kDa).

matrin *or* **DNA-binding protein F/G** a **zinc-finger** DNA-binding protein of the fibrogranular areas of the nucleus. Matrins comprise a family of eight major internal matrix polypeptides of nuclear matrices of rat liver and tissue culture cells, highly conserved between humans and mouse. Example from rat: database code MAFG_RAT, 544 residues (59.67 kDa). The name has sometimes been used as a synonym for **matrilysin** and matrin F/G is therefore used to avoid confusion.

matrix (*pl.* **matrices** *or* **matrixes**) **1** a medium or place wherein something is formed, develops, or is embedded or enclosed. **2** the medium that forms, or supports, the stationary phase in certain separative procedures, as in chromatography or zone electrophoresis; the material that forms, or is used to form, the substratum of an immobilized reagent in affinity chromatography. **3** *(in animal histology) see* **extracellular matrix**. **4** *(in plant histology)* the meshwork of solubilizable substances, largely polysaccharide in nature, occurring in cell walls and in which insoluble microfibrils of cellulose are embedded. **5** *see* **mitochondrial matrix**. **6** cytoplasmic matrix; *see* **groundplasm**. **7** the substratum, living or nonliving, in or on which a fungus or lichen grows. **8** *(in mathematics)* any rectangular array of numbers or symbols manipulable algebraically as a single entity and used according to specific rules to facilitate solving of certain kinds of problems, e.g. a set of simultaneous linear equations.

matrix Gla protein a protein that mediates association of the organic matrix of bone and cartilage. It contains γ-carboxyglutmate (Gla) residues, formation of which is vitamin-K-dependent. Example (precursor) from human: 103 amino acids (12.31 kDa).

matrix metalloproteinase *abbr.*: MMP; *a name given to* proteolytic enzymes associated with the **extracellular matrix** as the basis of a new nomenclature for these enzymes. The classification includes: MMP1, interstitial collagenase; MMP2, gelatinase A; MMP3, stromelysin-1; MMP8, neutrophil collagenase; MMP10, stromelysin-2; MMP12, metalloelastase. Such metalloproteinases have been implicated in clearing a path through the extracellular matrix for cell migration, and thus have been thought to be involved in the ability of malignant cells to invade tissues and metastasize. They have also been shown to be involved in conversion of tumour necrosis factor (TNF) precursor into active TNF and may be implicated in other diseases such as rheumatoid arthritis or osteoarthritis. For these reasons, there is current interest in matrix metalloproteinase inhibitors (*abbr.*: MMPIs) as potentially useful drugs. *See also* **TIMP**.

matrix metalloproteinase inhibitor *see* **MMPI**.

matrix processing peptidase *abbr.*: MPP; *an alternative term for* **mitochondrial processing peptidase**.

matrix protein **1** the major protein component of the outer membrane of *Escherichia coli*. It is a transmembrane protein that forms hydrophilic pores permitting the passage of microsolutes through the outer membrane; in association with **lipopolysaccharide** (def. 4) it forms a receptor for phages. It is a member of the **porin** family, and is a product of the gene *DMPC*: database code DMPC_ECOL1, 367 amino acids (40.39 kDa). **2** any of a class of proteins that coat the inside of the lipid bilayer in the envelope of some groups of enveloped viruses.

matrix space *or* **(mitochondrial) lumen** the innermost compartment of a mitochondrion, containing the **mitochondrial matrix**.

matrix vesicle any of the minute, membrane-bound, extracellular particles (≈100 nm in diameter) occurring in the interstitial matrix of calcifying cartilage. The vesicles contain a number of enzymes involved with local calcification mechanisms.

maturation **1** the process of coming to full development, ripening, or becoming mature. **2** *or* **maturation division** the processes of formation of gametes (sperm or ova) from primary

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gametocytes involving meiosis of the nucleus with reduction of chromosome number from diploid to haploid. **3** *(in virology)* the overall process leading to the incorporation of a viral genome into a capsid and the development of a complete virion.

maturation-promoting factor *an alternative name for* **M-phase-promoting factor**.

maturation protein *or* **A protein** one of the three proteins coded for by certain single-stranded RNA bacteriophages, one molecule of which is necessary for proper encapsulation of the RNA and for binding of the phage to a pilus on the host cell. Example from bacteriophage fr: database code VASS_BPFR, 393 amino acids (43.96 kDa).

maturity-onset diabetes *a former name for* type 2 **diabetes mellitus**.

max *abbr. for* maximal or maximum.

MAX the symbol for a gene family coding for DNA-binding proteins that function in cell growth control. The product, Max, forms heterodimers with Myc (*see* ***MYC***) that bind specifically to CACGTG; it also forms homodimers of similar specificity. Max contains **helix-turn-helix** and hydrophobic heptad repeats. Database code MAX_HUMAN, 160 amino acids (18.27 kDa).

Maxam–Gilbert method (for DNA sequencing) *see* **chemical cleavage method**.

maxicell *or* **maxi cell** a bacterial cell that has been heavily irradiated with UV light and in which the chromosomal DNA is extensively degraded. Any plasmid(s) present usually escape damage and the genes they encode can be expressed.

maxicircle DNA any large, closed circular DNA molecule, as in the **kinetoplast** of *Leishmania tarantolae*.

maxima a plural of **maximum** (def. 1).

maximal *abbr.*: max; of, pertaining to, or reaching a maximum; being the greatest possible in size, duration, etc.; **maximum** (def. 2). —**maximally** *adv.*

maximal agonist effect *or* **intrinsic activity** *symbol*: α; the maximal effect that an agonist, whether conventional or inverse, can elicit in a given tissue under particular experimental conditions, expressed as a fraction of that produced by a full agonist acting through the same receptors under the same conditions.

maximal rate *or* **maximum rate** *another name for* **limiting rate** (now recommended).

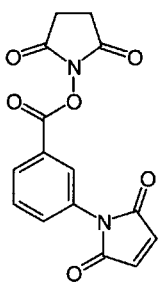
maximal velocity *or* **maximum velocity** *an older name for* **limiting rate**.

maximum *abbr.*: max; **1** (*pl.* **maxima** *or* **maximums**) the highest or greatest possible amount, degree, etc.; the highest value of a variable quantity. *Compare* **minimum**. **2** of, being, or exhibiting a maximum or maxima; **maximal**.

Maxwell relation a relation between the dielectric constant, ε, and the refractive index, n, of a nonabsorbing, nonmagnetic material such that $\varepsilon = n^2$. [After James Clerk Maxwell (1831–79), British physicist.]

Mb **1** *abbr.* and *symbol for* myoglobin; hence MbO_2, oxymyoglobin; MbCO, carbonmonoxymyoglobin; etc. **2** *symbol for* megabase, i.e. = 10^6 bases. **3** *(in computing) abbr. for* megabyte (i.e. 2^{20} bytes; alternative to MB).

MBS *abbr. for meta*-maleimidobenzoyl-*N*-hydroxysuccinimide ester; a heterobifunctional reagent useful, *inter alia*, for coupling an enzyme to an antibody, without appreciable loss of either activity.



MBSA *abbr. for* methylated bovine serum albumin.

mc *(formerly) abbr. for* millicurie (mCi now used).

Mc_3 *symbol for* mucotriaose ($McOse_3$ preferred if space permits).

Mc_4 *symbol for* mucotetraose ($McOse_4$ preferred if space permits).

MCAD *abbr. for* medium chain acyl-CoA dehydrogenase; *see* **beta-oxidation system**.

McArdle's disease *an alternative name for* type V **glycogen disease**.

McClintock, Barbara (1902–92), US geneticist noted for her studies on chromosome breakage and reunion and her proposal of the existence of transposable elements, Nobel Laureate in Physiology or Medicine (1983) 'for her discovery of mobile genetic elements'.

MCD *abbr. for* **1** magnetic circular dichroism. **2** mean corpuscular (erythrocyte) diameter.

MCDP *abbr. for* mast cell degranulating peptide.

McFarlane's method a method for the radioiodination of proteins with high efficiency in which the protein to be labelled is reacted with iodine monochloride that has been previously equilibrated with radioiodide. The extent of substitution can be precisely controlled by use of an appropriate quantity of iodine monochloride. [After Arthur Sproul McFarlane (1905–78), British biophysicist.]

mCi *symbol for* millicurie.

McIlwain chopper *or* **McIlwain–Buddle chopper** a hand- or motor-driven machine for rapidly cutting a piece of animal tissue into slices of uniform, preselected thickness (≥0.07 mm) and then, if desired, into prisms by making a second series of cuts. Such prisms can yield easily dispensed suspensions that retain those metabolic characteristics that tend to be lost on homogenization of tissue. [After Henry McIlwain (1912–92), British biochemist, and H. L. Buddle.]

McIntosh and Fildes jar *see* **anaerobic jar**.

McLeod gauge a mercury-in-glass vacuum pressure gauge that is capable of measuring down to 10^{-5} mmHg (1.33×10^{-3} Pa). A known large volume of gas is compressed into a small volume, in which the now much larger pressure is measured.

$McOse_3$ *symbol for* mucotriaose (preferred alternative to Mc_3).

$McOse_4$ *symbol for* mucotetraose (preferred alternative to Mc_4).

MCP *abbr. for* methyl-accepting chemotaxis protein.

Md *symbol for* mendelevium.

MD *(in clinical chemistry) abbr. for* **malate dehydrogenase** (def. 1).

MDa *abbr. for* megadalton.

MDCK cell *abbr. for* Madin–Darby canine kidney cell; a cell of a heteroploid cell line.

MDH *abbr. for* **malate dehydrogenase** (def. 1).

Mdm2 protein a nuclear phosphoprotein that binds to **p53** and inhibits its action. Example MDM2_MOUSE, 489 amino acids (54.54 kDa).

MDMA *abbr. for* 3,4-methylenedioxymethamphetamine.

MDP *abbr. for* muramyl-dipeptide.

MDR *abbr. for* multiple drug resistance *or* multidrug resistance; the acquired simultaneous resistance to a wide spectrum of drugs arising from the administration, typically over long periods, of one or a limited number of drugs. Such resistance may extend to drugs with little structural or even functional similarity to the original drug(s), and results in reduced efficacy of all the drugs concerned. The phenomenon is seen, e.g., in long-term chemotherapy of cancer patients, and is due to the induced expression of plasma membrane glycoproteins known as P-glycoproteins, or **MDR proteins**.

MDR protein any of several integral transmembrane glycoproteins of the **ABC** type that are involved in (multiple) drug resistance (*see* **MDR**). MDR 1 (or P-glycoprotein 1) is an energy-

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dependent efflux pump responsible for decreased drug accumulation in multidrug-resistant cells. Example from human: database code MDR1_HUMAN, 1280 amino acids (141.34 kDa). MDR 3 (or P-glycoprotein 3) is an energy-dependent efflux pump that causes decreased drug accumulation but is not capable of conferring drug resistance by itself. Example from human: database code MDR3_HUMAN, 1279 amino acids (140.52 kDa). MDR-associated protein participates in the active transport of drugs into subcellular organelles. Example from human: database code MRP_HUMAN, 1531 amino acids (171.47 kDa). MDR protein (or P-glycoprotein) of *Leishmania tarentolae* is a protein responsible for acquired methotrexate resistance, and is encoded by a gene located in the 'H-circle', a 68 kb duplex DNA circle containing a 30 kb inverted repeat. Database code MDR_LEITA, 1548 amino acids (172.04 kDa).

Me *symbol for* the methyl group, CH_3–.

Mead acid *a name sometimes given to* (*all-Z*)-eicosa-5,8,11-trienoic acid. It can be synthesized *de novo* by mammals via palmitate and oleate, and is thought to substitute partially for the long-chain polyunsaturated fatty acids lacking in essential fatty acid deficiency. [After J. F. Mead, who first identified it as an acid found in elevated concentrations in mammals during essential fatty acid deficiency].

mean *or* **arithmetic mean** *or* **average** the quotient of the arithmetic sum of any set of two or more numbers, measurements, values, etc. and the number of components of the set. *See also* **geometric mean**. *Compare* **median** (def. 1).

mean deviation the arithmetic average of the absolute values of the differences between the individual values of a set of numbers, values, etc. from their mean.

mean free path the average distance travelled by a molecular entity between collisions. In a gas, the mean free path between molecular entities is inversely proportional to the pressure of the gas.

mean ionic activity coefficient *symbol*: $\gamma_{\pm}$; the average rational activity coefficient of the ions of an electrolyte that dissociates in solution into cations of charge z^+ and anions of charge z^-, given, according to the limiting law of the Debye–Hückel theory, by:

$$-\log\gamma_{\pm} = z^+ z^- A I^{0.5},$$

where A is a constant whose magnitude depends on temperature, dielectric constant, etc., having a value near 0.5, and I is the ionic strength of the solution.

mean life *or* **average life** *abbr.*: τ; the mean of the lengths of time required for the disintegration of all atoms of a given radionuclide. It is related to the **half-life**, $t_{½}$, and to the **disintegration constant**, λ, of the radionuclide by the expressions:

$$\tau = t_{½}/\ln 2 = 1.443 t_{½},$$

and

$$\tau = 1/\lambda.$$

mean relative residue mass *or* *(formerly)* **mean residue weight** *symbol*: M_o; the quotient of the relative molecular mass of a polymer and the number of residues it contains.

mean residue rotation the average molar optical rotation for a residue in a polymer. It is obtained by substituting the mean relative residue mass, M_o, for the relative molecular mass, M_r, of the polymer in the equation defining **molar optical rotation**.

mean residue weight *a former name for* **mean relative residue mass**.

Mec *abbr. for* the 4-methylcoumarin-7-yl group.

mechanical concerned with, executed or operated by, or as by, a machine; relating to mechanics. —**mechanically** *adv.*

mechanically gated channel *see* **ion channel**.

mechanics **1** the science concerned with the equilibrium or motion of bodies in a given frame of reference. **2** the science of machines and/or machinery.

mechanism **1** the chain of events in a particular process; the action or process by which an effect is produced or an action performed. **2** *(in chemistry)* the detailed description of the pathway leading from reactants to products of a reaction, including where possible a characterization of the composition, structure, and other properties of any reaction intermediates and transition states. **3** any system or structure of moving parts that performs some function; a machine.

mechanistic of, pertaining to, or explained by mechanics; of, pertaining to, or resembling a mechanism. *Compare* **stochastic**.

mechanochemical coupling the coupling of a chemical process with a mechanical process in the same structure. *See also* **motor protein**.

meconium antigen *see* **carcinoembryonic antigen**.

Medawar, (Sir) Peter Brian (1915–87), British zoologist and immunologist; Nobel Laureate in Physiology or Medicine (1960) jointly with F. M. Burnet 'for discovery of acquired immunological tolerance'.

media **1** a plural of **medium**. **2** *(in morphology) or* **tunica media** the middle layer of the wall of a blood or lymph vessel.

medial **1** of, situated in, or towards the middle. **2** of, or pertaining to, a **media** (def. 2).

median **1** *(in statistics)* the centre value of any series of numbers, measurements, values, etc. when these are arranged in order from the lowest value to the highest value (with an even-numbered series, the mean of the two central values is taken); i.e. half the members of the series have values greater than that of the median and half have values smaller than that of the median. *Compare* **mean**. **2** of, pertaining to, situated in, or pointing towards the middle. **3** *(in biology)* of or pertaining to the plane that divides an organism, organ, etc. into two symmetrical parts.

median effective dose *abbr.*: ED_{50} *or* ED50; the dose of a drug, agonist, or other agent that is effective in 50% of the test objects.

median infectious dose *abbr.*: ID_{50} *or* ID50; the dose of bacteria, viruses, or other infective agents that produces infection in 50% of the test objects.

median lethal dose *abbr.*: LD_{50} *or* LD50; the dose of bacteria, viruses, toxic substances, or other agents that causes death of 50% of the test objects.

mediated transport the transport of a substance across a (biological) membrane that requires the participation of one or more transporting agents (or **carriers** (def. 3)). *See also* **facilitated diffusion**.

medical of, or pertaining to, the science or practice of medicine.

medicinal pertaining to or possessing therapeutic properties.

medicine **1** the science or practice of preventing, diagnosing, alleviating, and curing disease. **2** *a common term for* a pharmaceutical substance or mixture.

medium (*pl.* **media** *or* **mediums**) **1** the surrounding substance in which organisms or cells are studied or preserved. **2** the continuum in which particular chemical entities and their reactions are studied, commonly the solvent together with any nonreacting solutes. **3** any of the materials in which a chromatographic or an electrophoretic separation is effected. **4** the continuum through which electromagnetic radiation is considered to be transmitted. **5** *see* **culture medium**.

MEDLINE a US computerized science bibliography related to *Index Medicus*, that contains medical and many biochemical and biological references.

medulla (*pl.* **medullas** *or* **medullae**) the innermost part of an organ, tissue, or structure; marrow, pith. —**medullary** *adj.*

mega+ **1** *symbol*: M; an SI prefix denoting 10^6 times. **2** a prefix used in computing to indicate a multiple of 2^{20} (i.e. 1 048 576), as in megabyte. **3** *a general prefix* denoting large size.

Mega-8 *or* **Omega** the octanoyl amide of *N*-methylglucamine (i.e. 1-methylamino-1-deoxy-D-glucitol); a water-soluble, non-denaturing detergent (CMC = 58 mM) useful for membrane research. It is one of a series, which also comprises Mega-9, the nonanoyl derivative (CMC = 19–25 mM), and Mega-10, the decanoyl derivative (CMC = 6–7 mM).

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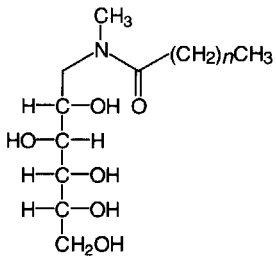

Mega-8 $n = 6$
Mega-9 $n = 7$
Mega-10 $n = 8$

megabase *symbol*: Mb; a unit of length of a polynucleotide equal to 10^6 base residues in a single-stranded polynucleotide or 10^6 base pairs in a double-stranded polynucleotide.

megadalton *symbol*: MDa; a unit of mass equal to 10^6 **daltons**.

megakaryocyte a large (diameter 40–150 μm), polyploid cell that gives rise to the blood platelets by budding of its cytoplasm. It contains, on average, four times the diploid number of chromosomes in a large, usually lobulated nucleus. Megakaryocytes are found in bone marrow, lung, and to a lesser extent in other tissues.

megaloblastic anemia any of a group of disorders characterized by an abnormality of red cell development in the bone marrow. There is an accumulation of primitive cells, with failure of nuclear development, while cytoplasmic development, including hemoglobinization, continues; oval macrocytes appear in the blood. Vitamin B_{12} or folate deficiency, or abnormality of vitamin B_{12} or folate metabolism, is a frequent cause, but drug treatment (with antifolates, e.g. methotrexate, or drugs that interfere with DNA synthesis, e.g. cytarabine (β-cytosine arabinoside), hydroxyurea, AZT) or certain leukemias may also be causes.

megatomic acid *see* **tetradecadienoic acids**.

meiosis *or* **reduction division** a process by which the nucleus of a diploid cell divides twice with the formation of four daughter haploid cells, each containing half the number of chromosomes of the parent nucleus. Meiosis occurs during the formation of gametes from diploid cells and at the beginning of haplophase in those organisms that exhibit alternation of generations. Meiosis involves two rounds of cell division. Prophase in the first division proceeds as follows. Chromosomes first become visible as elongated threads during **leptotene**; by this time each chromosome has already replicated to form two identical sister chromatids. During **zygotene** each chromosome pairs with its homologue; the two become aligned and the **synaptonemal complex** develops between them. When synapsis is complete **pachytene** is said to have begun; it is during this stage that **crossing over** occurs between a chromatid in one partner and another chromatid in the homologous chromosome. The points of crossing over, or **chiasmata**, first become visible as the two chromosomes begin to separate in **diplotene**, when the synaptonemal complex dissolves. The final phase of prophase I, **diakenesis**, is the transition into metaphase I, which is analgous to mitotic metaphase and is followed by anaphase I and telophase I, producing two daughter cells each with one copy of each chromosome (each still made up of two sister chromatids). A second division quickly follows, comprising an interphase (without chromosome replication), and mitosis-like prophase II, metaphase II, anaphase II, and telophase II to separate the two chromatids in each chromosome. *Compare* **mitosis**. —**meiotic** *adj.*

MEK *abbr. for* methyl ethyl ketone.

melanin any of the black or brown pigments of high molecular mass formed by the action of oxidase enzymes on phenols. They are widely distributed in plants and animals and are usually bound to protein. The most important precursor of melanins is the phenolic amino acid **tyrosine**. Plant melanins are called **catechol melanins** because they yield catechol on alkali fusion; animal melanins, termed **eumelanins**, arise from the formal polymerization of indole-5,6-quinone and thus, in contrast to plant melanins, contain nitrogen. —**melanic** *adj.*

melanocortin *a generic term for* either of the peptide hormones **melanotropin** or **corticotropin**, deriving from the composite **proopiomelanocortin**, the polyprotein from which they are formed. Although the two hormones have distinct functions (melanotropin in control of melanocyte growth and pigment formation, corticotropin in stimulating the adrenal cortex to produce glucocorticoids and aldosterone), they also share functions in, e.g., immunomodulation and antipyretic activity; while corticotropin can regulate melanocyte function, it is thus possible also to regard it as a melanotropin.

melanocortin receptor similarities between the receptor structures for **corticotropin** (*abbr.*: ACTH) and **melanotropin** (*abbr.*: MSH) indicate that this is a subfamily of G-protein-coupled, adenylate cyclase-activating, seven-transmembrane-domain receptors. Several types of receptor have been identified: **melanocortin-1 receptor**, *other names*: melanocyte-stimulating hormone receptor; melanotropin receptor; located on melanocytes and adrenocortical tissue; example from human: database code MSHR_HUMAN, 317 amino acids (34.66 kDa); **melanocortin-2 receptor**, *other name*: adrenocorticotropic hormone receptor; located on melanocytes and adrenocortical tissue; example from *Bos taurus*: database code ACTR_BOVIN, 297 amino acids (33.29 kDa); **melanocortin-3 receptor**, located on brain, placental, and gut tissue; example from human: database code MC3R_HUMAN, 360 amino acids (40.11 kDa); **melanocortin-4 receptor**, located on brain, placental, and gut tissue; example from human: database code MC4R_HUMAN, 332 amino acids (36.95 kDa); **melanocortin-5 receptor**, expressed in brain but not melanocytes; example from human: database code MC5R_HUMAN, 325 amino acids (36.6 kDa). Human ACTH receptor is 39% identical with the human MSH receptor. Receptors 1–3 and 5 respond to α-, β-, and γ-MSH and ACTH, melanocortin-4 receptor being specific to a common heptapeptide core sequence MGHFRWG. However, despite similarities in structure and action on melanocortin receptors, physiologically MSH has no ACTH-like activity. These are among the smallest G-protein-coupled receptors identified to date; they are more closely related to the Δ^9-tetrahydrocannabinol receptor (*see* **cannabinoid receptor**) than to other peptide and amine G-protein-coupled receptors.

melanocyte a type of pigmented cell that can synthesize and store **melanin** in melanosomes. Melanocytes occur in the skin and in the pigmented layer of the eye. *See also* **melanophore**.

melanocyte regulatory factor *an alternative name for* **melanotropin regulatory factor**.

melanocyte-stimulating hormone *abbr.*: MSH; any of three peptide hormones, α-MSH, β-MSH, and γ-MSH, produced primarily by the intermediate lobe of the pituitary gland, that cause dispersal of melanosomes in **melanophores** of poikilothermic vertebrates, but whose physiological function in mammals is not understood. Their sequences are all contained within that of **proopiomelanocortin** (the common precursor of corticotropin and β lipotropin). α-MSH is a tridecapeptide amide (usually acetylated on the N-terminal serine residue) that corresponds to residues 1–13 of corticotropin and has the same sequence in almost all animals studied. β-MSH (*formerly called* **intermedin**), not believed to be present in humans, corresponds to residues 41–58 of β lipotropin and shows greater structural variability. γ-MSH, a putative hormone, is a peptide of variable length that corresponds to part of the so-called cryptic region of proopiomelanocortin. *See also* **melanotropin**.

melanocyte-stimulating hormone receptor *see* **melanotropin receptor**.

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melanocyte-stimulating-hormone regulatory factor *or* **melanocyte-stimulating-hormone regulatory hormone** *an alternative name for* **melanotropin-regulatory factor**.

melanocyte-stimulating-hormone release-inhibiting factor (*abbr.*: MSHIF *or* MSHRIF) *or* **melanocyte-stimulating-hormone release-inhibiting hormone** (*abbr.*: MSHIH *or* MSHRIH) *an older name for* **melanostatin**.

melanocyte-stimulating-hormone releasing factor (*abbr.*: MSHRF) *or* **melanocyte-stimulating-hormone releasing hormone** (*abbr.*: MSHRH). *See* **MSHRH**.

melanoliberin *the recommended name for* melanocyte-stimulating-hormone releasing hormone (*see* **MSHRH**).

melanophore a type of **melanocyte** that occurs especially in the skin of poikilothermic vertebrates. The cell's contractile properties allow rapid internal translocation of melanosomes, thereby bringing about rapid adaptive changes in the skin coloration of such creatures.

melanosome a type of cellular organelle that occurs in **melanocytes**; melanosomes contain tyrosinase and can synthesize and store melanin.

melanostatin a substance identified by its ability to inhibit release of melanotropin; it is now known to be identical with **neuropeptide Y**. *Other names*: melanotropin release-inhibiting factor (*abbr.*: MIF *or* MRIF); melanotropin release-inhibiting hormone (*abbr.*: MIH *or* MRIH); melanocyte-stimulating-hormone release-inhibiting factor (*abbr.*: MSHIF *or* MSHRIF); melanocyte-stimulating-hormone release-inhibiting hormone (*abbr.*: MSHIH *or* MSHRIH).

melanotransferrin *see* **transferrin**.

melanotropic *or* **melanotrophic** describing any agent that causes dispersal of melanosomes within **melanophores**.

melanotropin *or (formerly)* **melanotrophin** *a generic term for* any melanotropic hormone of the anterior pituitary that is derived from **proopiomelanocortin**. The term embraces α, β, and γ **melanocyte-stimulating hormones**. *See also* **melanocortin**.

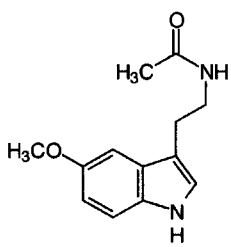
melanotropin receptor any of a family of receptors that bind **melanotropins**. *See also* **melanocortin receptor**.

melanotropin-regulatory factor *or* **melanotropin-regulatory hormone** *an older generic name for* either **MSHRH** or **melanostatin**. *Other names*: melanocyte-regulatory factor; melanocyte-stimulating-hormone regulatory factor; melanocyte-stimulating-hormone regulatory hormone.

melanotropin release-inhibiting factor (*abbr.*: MIF *or* MRIF) *or* **melanotropin release-inhibiting hormone** (*abbr.*: MIH *or* MRIH) *an older name for* **melanostatin**.

melanotropin-releasing factor (*abbr.*: MRF) *or* **melanotropin-releasing hormone** (*abbr.*: MRH) *see* **MSHRH**.

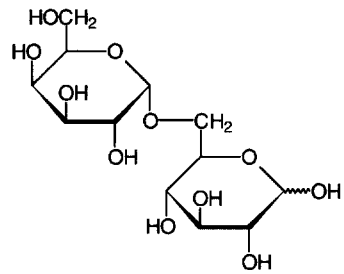
melatonin *N*-acetyl-5-methoxytryptamine; a neuroendocrine principle synthesized in the pineal gland from 5-hydroxytryptamine; its synthesis exhibits a circadian photoperiodism. In amphibia, it has an action opposite to that of **melanocyte-stimulating hormone**. It stimulates the aggregation of melanosomes in melanophores, thus lightening the skin. When used as a drug it is reputed to control jet lag.



melezitose the trisaccharide, *O*-α-D-glucopyranosyl-(1→3)-*O*-β-D-fructofuranosyl-(2→1)-α-D-glucopyranoside; a component of the sweet exudations from many plants and of the leaves of some trees after insect attack.

melibiase *see* **glucosidase**.

melibiose the disaccharide, 6-*O*-α-D-galactopyranosyl-D-glucose; it occurs as a constituent of the trisaccharide, **raffinose**, and in the exudates and nectaries of a number of plants.



melissyl *an alternative name for* **myricyl**.

melitriose *see* **raffinose**.

melittin a strongly basic, sulfur-free, hemolytic, 26-residue peptide amide, often formylated on its N-terminal glycine residue. It comprises 40–50% of the dry mass of the venom of the honey bee, *Apis mellifera*. The hemolytic activity of melittin appears to be related to the ordering of its amino-acid residues, which renders the polypeptide markedly surface active. Example from *A. mellifera*, chain A: database code NRL_2MLTA, 26 amino acids (2.84 kDa); chain B: database code NRL_2MLTB, 26 amino acids (2.84 kDa); both 3-D structures are known.

melting **1** the (reversible) act or process of liquefaction of a solid through the action of heat (or change in pressure). **2** the increase (reversible and usually fairly abrupt) of molecular mobility of lipids in a biological membrane or artificial lipid bilayer with increase of temperature above the transition temperature. **3** *or* **thermal denaturation** the transition (usually fairly abrupt but not necessarily reversible) of a biopolymer from a highly ordered to a less highly ordered state with increase in temperature. Examples are the heat-induced change from a helical to a random coil structure in a protein or a duplex nuleic acid. *See also* **localized melting**, **melting temperature**.

melting curve *an alternative name for* **thermal denaturation profile**.

melting point *abbr.*: m.p.; the temperature at which the solid and liquid phases of a substance are in equilibrium at a given pressure. Melting points are usually given for standard atmospheric pressure, i.e. 101 325 Pa.

melting temperature *symbol*: T_m *or* t_m *or* Θ_m; the temperature at which a conformational transition brought about by change in temperature, e.g. of a macromolecule in solution, is 50% complete. It follows therefore that $T_m = \Delta H_{ot}/\Delta S_{ot}$, where ΔH_{ot} and ΔS_{ot} are, respectively, the standard enthalpy difference and the standard entropy difference for the transition. In the denaturation of DNA the melting temperature is taken as the midpoint of the **helix-to-coil transition**.

MEM *abbr. for* **1** minimum essential medium. **2** minimum Eagle's medium.

membrane any thin sheet or layer, often separating two compartments. Membranes may be natural or artificial, and are sometimes soft and pliable. *See also* **cell membrane**, **semipermeable membrane**, **unit membrane**. —**membranous** *adj.*

membrane attack complex *see* **MAC** (def. 1).

membrane attack complex inhibition factor *abbr.*: MACIF *or* **CD59 glycoprotein precursor**; *other names*: MAC-inhibitory protein, protectin, membrane inhibitor of reactive lysis (*abbr.*: MIRL); a surface antigen of T cells that potently inhibits the membrane attack complex (*see* **MAC**). It is complexed with a GPI anchor. Example from human: database code CD59_HUMAN, 128 amino acids (14.18 kDa).

membrane-bound describing any component that is not readily dissociable from preparations of cellular membranes *in*

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vitro and/or that appears to be an integral part of a membrane in an intact cell.

membrane channel a protein complex that specifically facilitates the passive diffusion of small molecules through a membrane; particularly applied to **ion channels**.

membrane electrode any electrode that incorporates a membrane in its structure, e.g. a glass electrode, an ion-exchange electrode, or an oxygen electrode.

membrane filter *or* **filter membrane** any membrane consisting of a thin polymeric structure with pores of a defined and very uniform size that is used for filtration; a disk or piece of such membrane.

membrane filtration the act or process of separating suspended particles from a liquid, or of separating macromolecules from their solvent, with a **membrane filter**.

membrane-organizing spike protein *see* **moesin**.

membrane osmometer *see* **osmometer**.

membrane potential the electric potential existing across any membrane arising from charges in the membrane itself and from the charges present in the media on either side of the membrane. Plant and animal plasma membranes maintain a potential, the cell interior being more negative than the exterior. In plants this arises mainly from the activity of electrogenic pumps, whereas in animals passive ion movements predominate in creating this potential. The resting potential varies from –20 mV to –200 mV according to cell type; for a neuron it is about –70 mV. In plants, **H^+-transporting ATPases** pump protons out of the cell, thus maintaining a pH gradient across the plasma membrane. This is involved in symport of carbohydrates and amino acids into the cell. In animals, the Na^+,K^+-ATPase exchanges intracellular Na^+ for extracellular K^+, maintaining the high intracellular Na^+ for extracellular K^+ concentration and low intracellular Na^+ concentration. K^+-leak channels in the plasma membrane allow K^+ to escape until counteracted by the electrical potential and excess of intracellular negative charge that results. An electrochemical gradient across the mitochondrial inner membrane is created by proton-pumping cytochromes. *See also* **chemiosmotic coupling hypothesis**, **Nernst equation**.

membrane protein any protein that is normally closely associated with a cell membrane. Such an association results from a variety of properties of the protein and the method by which it is synthesized. **Integral proteins** contain hydrophobic regions that traverse the lipid bilayer; in some cases, the protein has only one such region, with hydrophilic domains on either side of the membrane; in other cases, where several such regions are present, a single polypeptide chain may traverse the membrane several times (*see* **seven-transmembrane-domain proteins**). Other proteins are bound to the membrane by a **GPI anchor**, and others by the hydrophobic moiety of a fatty-acyl group (*see* **myristoylation**) or a prenyl group (*see* **prenylation**). Other proteins may be more loosely attached, mainly by ionic forces (peripheral proteins).

Membrane-anchored proteins may be classified into a number of types, depending on the number of transmembrane domains, the orientation of the protein, and the presence of other kinds of attachment to the lipid bilayer. **Type I membrane proteins** have a single transmembrane domain, with the C terminus on the cytoplasmic side. **Type II membrane proteins** have a single transmembrane domain with an N terminus that is cytoplasmic. **Type III membrane proteins** have a single polypeptide chain that traverses the membrane several times. **Type IV membrane proteins** are made up of multimers of subunits that when assembled make a transmembrane channel. Proteins attached to the membrane only by covalently bound lipids are classified as **type V**, and those that are anchored by one or more transmembrane domains and also by a GPI anchor are designated **type VI**. The structures of only a few membrane proteins have been solved at high resolution (7 Å or better). Except for these it is not known whether the transmembrane domain is helical.

membrane receptor any of the many proteins, situated in or on a cell membrane, that bind extracellular signalling molecules (e.g. hormones, growth factors) and transduce the signal to intracellular effects.

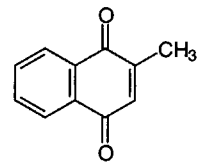
membrane skeleton the protein network of an erythrocyte membrane, defined operationally as the insoluble residue that remains after extraction of either intact red cells or their isolated membranes with the nonionic detergent Triton X-100.

membrane teichoic acid any **teichoic acid** found in the protoplast of a bacterial cell as opposed to any found exclusively in the cell wall or in capsular material. Such substances commonly are glycerol teichoic acids, and they occur, covalently attached to lipid, in the cell membrane and probably also in mesosomes.

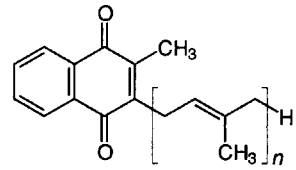
membrane transport any movement of substances across a (biological) membrane.

memory cell any of a population of long-lived **T** or **B lymphocytes** that have previously been stimulated by antigen, and make an accelerated response to that antigen if they encounter it again. Memory B cells carry surface immunoglobulin G as their antigen receptor; this is of higher affinity than on virgin lymphocytes. Memory T cells may be distinguishable by high expression of CD44.

menadione 2-methyl-1,4-naphthalenedione; 2-methyl-1,4-naphthoquinone; vitamin K_3; a synthetic naphthoquinone derivative possessing the physiological properties of **vitamin K**.



menaquinone *abbr.*: MK; *the class name for* a series of 2-methyl-3-all-*trans*-polyprenyl-1,4-naphthoquinones, also known as vitamins K_2 (*see* **vitamin K** for function). They are antihemorrhagic vitamins, present in bacteria, and possess 1–13 prenyl residues, the number of prenyl residues being indicated by a suffixed Arabic number, e.g. menaquinone-6 (MK-6; *also known as* **farnoquinone**). [From methyl naphthaquinone.]



Mendel, Gregor Johann (1822–84), Austrian monk and botanist. *See also* **Mendel's laws of heredity**.

Mendeleev *or* **Mendeleyev** *or* **Mendeléeff, Dmitri Ivanovich** (1834–1907) Russian chemist who proposed the **periodic law** and **periodic table**.

Mendelian **1** of or relating to **Mendel**, or following his laws of heredity. **2** one who adheres to or supports **Mendel's laws of heredity**.

Mendel's laws of heredity the principles of heredity proposed by Gregor **Mendel** on the basis of his researches on hybridization of peas to explain the behaviour of factors (now called genes) that govern the transmission of inherited characters from generation to generation. On the basis of modern knowledge, Mendel's first law, the **law of segregation**, states that every somatic cell carries a pair of allelic genes for each character and that the two genes in each pair separate during meiosis so that each gamete carries only one gene from each

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pair. Mendel's second law, the **law of independent assortment**, states that the separation of members of any pair of allelic genes occurs independently of every other pair provided they are not linked.

meniscus (*pl.* **menisci**) the curved upper surface of a liquid column that is concave when the containing walls are wetted by the liquid (contact angle <90°) or convex when not (contact angle >90°), sometimes extended to include a flat surface (contact angle = 90°). —**meniscoid** *adj.*

meniscus depletion (sedimentation equilibrium) method *or* **Yphantis method** a variant of the sedimentation equilibrium method for determining the relative molecular mass of a macromolecule in which centrifugation is effected at a speed high enough to render the concentration of the solute at the meniscus essentially zero; the concentrations of solute along the length of the cell are proportional to the difference in refractive index at any point from that at the meniscus. The method is especially useful for monodisperse systems.

Menke's disease *or* **kinky-hair syndrome** *or* **steely-hair syndrome** a genetically determined defect of copper metabolism found in some humans. Most of the clinical and pathological manifestations can be explained on the basis of a profound copper deficiency caused by an inability to absorb copper from the gastrointestinal tract and also, probably, to a reduced ability to absorb copper from the mother during intrauterine life.

menopausal gonadotropin *or* **human menopausal gonadotropin** (*abbr.*: hMG *or* HMG); *another name for* **menotropin**.

menotropin *or* **menotrophin** *other name*: human menopausal gonadotropin; *abbr.*: hMG *or* HMG; a gonadotropin with **follicle-stimulating hormone** and **luteinizing hormone** activity, isolated from the urine of postmenopausal women and used to stimulate ovulation in infertility. One proprietary name is Pergonal.

Menten, Maude Leonora (1879–1960), Canadian physician, biochemist, and experimental pathologist; best known for her collaboration with Leonor **Michaelis** in the formulation of Michaelis–Menten kinetics of enzyme action (*see* **Michaelis kinetics**).

MEP *abbr. for* major excreted protease; *see* **cathepsin L**.

meprin A EC 3.4.24.18; *other names*: endopeptidase-2; endopeptidase MEP-1; a metalloendopeptidase of the membranes of kidney and intestinal brush borders. It is an integral protein with the catalytic domain lying towards the exterior. Zinc is a cofactor. It catalyses the hydrolysis of proteins and peptides on the C-terminal side of hydrophobic residues, and is a homotetramer of α or β subunits. Example: precursor of mouse α-subunit (mep-1): database code MEPA_MOUSE, 760 amino acids (85.61 kDa); theoretical 3-D model of this: database code NRL_1IAF, 198 amino acids (22.88 kDa).

meq *or* **mEq** *symbol for* milliequivalent (use deprecated, mmol recommended).

mer *or* **constitutional unit** the repeating unit of a polymeric molecule.

+mer *suffix forming nouns (in chemical nomenclature)* denoting specific kinds or classes of polymer (e.g. hexamer, oligomer) or isomer (e.g. enantiomer, epimer, tautomer). —**+meric** *adj.*; **+merism** *n.*

mer the symbol for genes of the *mer* operon whose products confer (or regulate) mercury resistance. The following examples are of *mer* products from *Serratia marcescens*. (1) MerA: mercury II reductase (EC 1.16.1.1); *systematic name*: Hg:NADP$^+$ oxidoreductase; one of the very rare enzymes with metal substrates, it catalyses the reduction by NADPH of Hg^{2+} to form Hg and $NADP^+$. It is a flavoprotein (FAD) with redox-active disulfide bonds; homodimer: database code MERA_SERMA, 460 amino acids (48.53 kDa). This enzyme is responsible for volatilizing mercury as Hg(0). (2) MerB: alkylmercury lyase (EC 4.99.1.2); *systematic name*: alkylmercury mercuric-lyase; it catalyses a reaction between RHg^+ and H^+ to form RH and Hg^{2+}. This enzyme cleaves the carbon–mercury bond of organomercurials and the Hg^{2+} product is detoxified by MerA. Database code MERB_SERMA, 212 amino acids (23.05 kDa). (3) MerR: this is a **helix-turn-helix** regulatory protein: database code MERR_SERMA, 144 amino acids (16.01 kDa). In the absence of mercury, MerR represses transcription by binding tightly to the *mer* operator region; when mercury is present the dimeric complex binds a single ion and becomes a potent transcriptional activator, while remaining bound to the *mer* site. *mer* operons are encoded by a number of plasmids which have been cloned into *Escherichia coli*, e.g. Tn21 of *Shigella flexneri*, Tn501 from *Pseudomonas aeruginosa* (these two lack the organomercury lyase gene and so confer resistance only against inorganic mercury salts), and pDU1358 from *S. marcescens* (which includes *merB* and thus encodes a broad spectrum *mer* operon).

mer+ *prefix (in coordination compound nomenclature)* denoting a **meridional** (def. 2) arrangement of ligands.

MER *abbr. for* medium reiteration frequency repeat; *other usage*: medium reiteration frequency interspersed repetitive elements (*abbr.*: MER elements). They consist of repeated base sequences in eukaryotic genomes. More than fifty human repetitive families are known, of which most represent MERs. The latter have copy numbers per genome ranging from hundreds to thousands, and length ranging from tens to a few hundred base pairs. They are of unknown function, but some may play a role in regulation of gene expression and others may affect genome stability and gene rearrangements.

mercapt+ *a variant form of* **mercapto+** *(sometimes before a vowel)*.

mercaptan *an old name for* **thiol**.

mercapto+ *or (sometimes before a vowel)* **mercapt+** *comb. form (in chemical nomenclature)* indicating the presence of an unsubstituted thio group, –SH.

2-mercaptoethanol HO–CH_2–CH_2–SH; 2-hydroxyethylmercaptan; a sulfhydryl reducing agent often used in buffers to maintain protein sulfhydryl groups in the reduced state.

mercaptopurine *or* **6-mercaptopurine** *abbr.*: 6-MP; *symbol*: Shy; thiohypoxanthine; 6-purinethiol; an immunosuppressive and antineoplastic drug useful in organ transplantation and in the treatment of some leukemias. It is a substrate for guanine-hypoxanthine phosphoribosyltransferase, which converts it to **6-mercaptopurine ribonucleoside** (or 6-thioinosine; *symbol*: Sno *or* M *or* sI).

mercapturic acid any *S*-alkyl- or *S*-aryl-*N*-acetylcysteine; such compounds are formed as detoxification products in mammals. The initial reaction involves conjugation with the thiol group of glutathione catalysed by a **glutathione transferase** to form the *S*-radyl-glutathione (*see* **radyl**). Glutamic acid and glycine are then removed in the kidney, and the resulting mercapturic acid is excreted in the urine.

mercurate to treat or mix with mercury; to introduce mercury into an organic compound. —**mercuration** *n.*

mercurial **1** of, containing, like, or pertaining to mercury. **2** any compound containing mercury, especially one used in medicine and/or agriculture; *see also* **organomercurial**.

mercuric perchlorate $Hg(ClO_4)_2$; a substance used in solution to trap ethylene.

mercury II reductase EC 1.16.1.1; product of the *Serratia marcesens merA* gene (*see* ***mer***).

mercury-vapour lamp *or* **mercury-discharge lamp** *or (informally)* **mercury lamp** a lamp that emits bluish-green light rich in ultraviolet radiation, produced by passing an electric discharge through mercury vapour, often at low pressure. It is useful for provoking or investigating fluorescence, as a light source for a **polarimeter**, and as a source of sterilizing radiation.

meridian **1** any line on the surface of a sphere or spheroid that is orthogonal to its equator, or any corresponding line in a projection of part of the surface of a sphere or spheroid onto a planar or cylindrical surface. **2** in a fibre diagram produced by X-ray diffraction, the vertical axis on the film that corresponds to the *z* axis in reciprocal space.

meridional **1** of, along, pertaining to, or resembling a meri-

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dian. **2** describing the geometrical isomer of a coordination compound of octahedral configuration in which three ligands in the coordination sphere are in such a relationship that one is *cis* to the two others, which are themselves *trans*. Such an isomer is designated by prefixing *mer-* to the chemical name.

meristem a region of tissue in a plant that is composed of one or more undifferentiated cells that are capable of undergoing mitosis and differentiation, and thereby of effecting growth and development of a plant by giving rise either to more meristem or to specialized tissue. In vascular plants, meristems may be apical (located at the tips of growing roots and shoots) or lateral (arranged circumferentially and constituting the cambium). —**meristematic** *adj.*

merlin *or* **neurofibromatosis type 2 (tumour suppressor)** (*abbr.*: NF2) *or* **Schwannomin** a membrane-stabilizing protein from fetal brain, and other tissues such as kidney, lung, and breast. It is similar to **ezrin** and **talin**. Example from human: database code MERL_HUMAN, 595 amino acids (69.61 kDa). It is a tumour suppressor of the **TERM** family. In the human, it is encoded by a gene on chromosome 22q12. Mouse complete sequence: database code MUSNF2D, 596 amino acids (69.61 kDa).

mero+ *comb. form* denoting part, partly, or partial.

merocrine **1** describing a type of secretion that does not entail disintegration of the secretory cell. **2** describing a gland made up of such cells. *Compare* **apocrine**, **eccrine**, **holocrine**.

merodiploid a haploid organism that is diploid for a small region of the chromosome, i.e. a partial diploid.

meromyosin either of the two fragments, **heavy meromyosin** and **light meromyosin**, produced by brief treatment of myosin with trypsin or certain other proteinases.

mero-receptor the smallest subunit of a receptor for a (steroid) hormone that contains an intact hormone-binding site. The biological significance of mero-receptors is unclear; they may be artefacts of experimental cellular disruption or products formed by proteolysis associated with the termination of (steroid) hormone action.

merosin a tissue-specific-basement-membrane protein, and the M chain of **laminin**. It is covalently associated with laminin B chains and like laminin is cruciform. It has homology to the C-terminal part of the laminin A chain. Example from human: database code HSLAMMMER, 3110 amino acids (342.38 kDa).

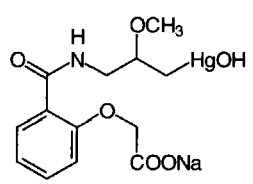
merozygote any bacterial cell that is partly diploid and partly haploid, formed by conjugation, transduction, or transformation. It contains one complete genome, that of the recipient organism, and a fragment of a second genome, derived from the donor.

Merrifield, Robert Bruce (1921–), US peptide chemist and biochemist; Nobel Laureate in Chemistry (1984) 'for his development of methodology for chemical synthesis on a solid matrix'.

Merrifield method *an alternative name for* **solid-phase peptide synthesis**.

Merrifield resin a beaded reactive synthetic resin designed for use in the Merrifield method (i.e. **solid-phase peptide synthesis**).

mersalyl *pharmaceutical name of* sodium *o*-{[3-(hydroxymercuri)-2-methoxypropyl]carbamoyl}phenoxyacetate; a mercury-containing derivative of salicylamide. It is a diuretic drug useful as an inhibitor of the exchange of phosphate and hydroxide ions across the inner mitochondrial membrane.



mes+ *a variant form of* **meso+** *(sometimes before a vowel).*

Mes *or* **MES** *abbr. for* and *trivial name of* 2-(*N*-morpholino)ethanesulfonic acid; a **Good buffer substance**, pK_a (20 °C) = 6.15.

mesaconic acid (*E*)-2-methyl-2-butenedioic acid; methylfumaric acid; an intermediate in the fermentation of glutamate to acetyl-CoA by *Clostridium tetanomorphum*.

mescaline 3,4,5-trimethoxyphenylethylamine; a hallucinogenic and sympathomimetic drug isolated from the flowering heads of the mescal cactus (*Lophophora williamsii*), also known as peyotle or peyote.

Meselson–Stahl experiment a landmark experiment, reported by Meselson and Stahl in 1958, that provided convincing evidence for semiconservative replication of DNA in bacteria. Cultures of *Escherichia coli* were grown in a medium containing $^{15}NH_4Cl$ (96.5% isotopic purity) as sole nitrogen source for many generations so as to label the DNA with heavy nitrogen. The cells were then transferred to a medium containing $^{14}NH_4Cl$ and the culture sampled for several subsequent generations. Cell lysates were subjected to density-gradient centrifugation and the positions of the DNA bands in the gradients located by UV absorption. Initially the DNA appeared as a single band corresponding to DNA containing heavy nitrogen; subsequently a second band of DNA, containing equal amounts of heavy and light nitrogen, appeared, and one generation after transfer to natural ammonium chloride all the DNA was this hybrid form. After two generations only hybrid and natural DNA was present. Furthermore, the separated strands of this hybrid DNA proved to contain all heavy nitrogen or all normal nitrogen only. [After Matthews Meselson (b. 1930), US molecular biologist, and Franklin William Stahl (b. 1929), US geneticist.]

mesenchyme immature, unspecialized connective tissue found in the early embryo of animals. It consists of cells embedded in a tenuous extracellular matrix. —**mesenchymal** *adj.*

mesentery **1** the double-layer fold of peritoneum serving to hold the abdominal viscera in position. **2** any of the muscular partitions extending inwards from the body wall in coelenterates. —**mesenteric** *adj.*

Me_3Si *symbol for* the trimethylsilyl group.

meso describing a bridging atom or group between two rings in a polycyclic molecule.

meso+ *or (sometimes before a vowel)* **mes+** *comb. form* denoting middle, or intermediate.

meso- *abbr.*: *ms-*; *prefix* (*in chemical nomenclature*) designating a substance whose individual molecules contain equal numbers of enantiomeric groups, identically linked, but no other chiral group; i.e. a substance whose molecules are optically inactive because of internal compensation; e.g. *meso*-compound, *meso*-cystine. *Compare* ***racemo-***.

***meso*-carbon atom** *a term suggested for* any prochiral carbon atom in an organic molecule whose valence bonds are linked to two identical groups, *a*, and to two other dissimilar groups, *b* and *d*. The resulting molecule, *Caabd*, has a plane of symmetry and thus the carbon atom is not chiral; however, the two *a* groups are not geometrically equivalent but bear a mirror-image relationship to each other, and they may react at different rates with chiral reagents or in enzymic reactions. The term is now obsolete. See **prochiral**.

mesoderm the middle of the three primary germ layers of a triploblastic animal embryo, lying between the ectoderm and endoderm. It is the source of bone, muscle, connective tissue, the inner layer of the skin, and other structures. —**mesodermal** *adj.*

***meso*-inositol** *a former name for* ***myo*-inositol**.

mesomeric effect *(in chemistry)* an experimentally observable effect (on reaction rates, etc.) of a substituent caused by the overlap of its p- or π-orbitals with the p- or π-orbitals of the rest of the molecular entity, **resonance** (def. 2) (or mesomerism) being thereby introduced into, or extended within, the molecular entity in question. *Compare* **inductive effect**.

mesomerism *(in chemistry)* a term used to imply that the correct representation of the structure of a particular molecular

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entity is intermediate between two or more formal valence-bond representations (known as **contributing structures**); **resonance** (def. 2). —**mesomeric** *adj.*

mesomorphic **1** *(in chemistry)* existing in, designating, or pertaining to an intermediate state between a true liquid and a true solid that exists in a **liquid crystal**. **2** *(in biology)* having a form, size, or structure that is average, normal, or intermediate between extremes.

mesophase any phase of matter intermediate between a true liquid and a true solid that exists in a **liquid crystal**.

mesophil *or* **mesophile** any organism that thrives at moderate temperatures, between 20 and 40 °C. —**mesophil, mesophile,** *or* **mesophilic** *adj.*

mesophyll the internal parenchyma of a foliage leaf between the two epidermal layers; it is usually photosynthetic. —**mesophyllic** *adj.*

mesophyte any plant requiring moderate amounts of water for optimum growth. —**mesophytic** *adj.*

mesopore any pore (in a gel or porous solid) intermediate in size between a micropore and a macropore, i.e. of width in the range roughly 2.0–50 nm. —**mesoporous** *adj.*

mesosecrin a glycoprotein, M_r 46 000, secreted by human mesoderm-derived and endothelial cells in culture.

mesosome an intracellular, often complex, membranous structure found in many bacteria and probably formed by invagination of the plasma membrane. It is more complex and larger in Gram-positive organisms than in Gram-negative ones. Its function is unclear. —**mesosomal** *adj.*

mesothelium (*pl.* **mesothelia**) a layer of flat cells derived from mesoderm and found lining various body cavities. —**mesothelial** *adj.*

mesotocin [Ile^8]oxytocin; a neurohypophyseal hormone present in some nonmammalian vertebrates, so-named because it is intermediate in structure between **isotocin** and **oxytocin**. It may represent an ancestral molecule, which has been preserved in these groups of vertebrates but has undergone a single residue replacement in mammals.

mesotrophic describing an environment providing a moderate amount of nutrients.

message **1** a specific piece of information, or something containing information, that is transmitted from a donor to a recipient by some means or agent. **2** a jargon term used, sometimes without an article, as the name of a substance, to denote the particular **messenger RNA** (mRNA) of interest in a specified context, or any preparation containing that mRNA. **3** the segment of mRNA (or any particular segment of a polycistronic mRNA) that consists of a sequence of codons carrying the information determining the sequence of amino-acid residues of a specific polypeptide to be synthesized at a ribosome. **4** the part of the information contained within the amino-acid sequence of a hormonal polypeptide, or of its biosynthetic precursors, that elicits a specific physiological response to the hormone. *Compare* **address** (def. 2).

message-dependent (of a partially purified, cell-free, protein-synthesizing system) capable of a significant response to added mRNA.

message sequence *or* **message region** the segment (or segments) of the complete sequence of amino-acid residues of a molecule of a hormonal or prohormonal polypeptide in which the **message** (def. 4) resides. *Compare* **address sequence**.

messenger **1** something, or someone, that bears or carries a **message** (def. 1), or that is able to do so. **2** a molecule or substance that carries genetic information; *see* **messenger RNA**. **3** a molecule or substance that carries physiological instructions; a **rheoseme**. *See also* **chemical messenger**, **first messenger**, **second messenger**.

messenger ribonucleoprotein *abbr.*: mRNP; any complex of messenger RNA (mRNA) and protein. Included are: nuclear ribonucleoprotein that contains mRNA sequences; cytoplasmic ribonucleoprotein that is associated with polyribosomes; and free cytoplasmic ribonucleoprotein particles, also known as **informosomes**.

messenger RNA *or* **template RNA** *abbr.*: mRNA; a class of naturally occurring RNA molecules that carry the information embodied in the genes of DNA to the ribosomes, where they direct protein synthesis. Molecules of mRNA are single-stranded, relatively short-lived, and formed by the process of **transcription** from the template strand of genomic DNA. They carry genetic information in the form of a succession of **codons**. At the ribosomes, by the process of **translation**, they orchestrate the synthesis of the corresponding polypeptide(s). The plus strand of certain RNA viruses can act as messenger RNA without transcription, as can a synthetic polyribonucleotide. The primary transcript of DNA is often referred to as **hnRNA** which contains the **introns** which have to be removed by excising and splicing together the **exons** to form the mature mRNA. mRNA may also undergo 'editing' whereby some bases are changed. *See also* **mRNA binding site**, **splicing**.

messenger-RNA-interfering complementary RNA *abbr.*: micRNA; *an alternative name for* **antisense RNA**.

Messing vector any one of certain cloning vectors derived from bacteriophage M13 by insertion of a synthetic multipurpose cloning site and which are especially suitable for the cloning and rapid sequence determination of small (≈500 base pair) fragments of DNA. These have developed into the **pUC vectors**. [After Joachim Messing (1946–).]

met+ *a variant form of* **meta+** (usually before a vowel or letter h).

Met *symbol for* a residue of the α-amino acid L-methionine (alternative to M).

MET a gene, first identified in an *N*-methyl-*N'*-nitrosoguanidine-treated cell line, that encodes a receptor tyrosine kinase with α and β subunits. The receptor binds **hepatocyte growth factor** and undergoes autophosphorylation of the cytoplasmic domain. Cells co-transfected with *MET* and *HGF* are highly tumorigenic. Example, database code KMET_HUMAN. *See also* **hepatocyte growth factor receptor**.

meta+ *or (before a vowel or letter h)* **met+** *prefix* **1** indicating alteration, alternation, or change of condition or position; after, distal to, behind, beyond; more highly specialized form of. **2** *(in inorganic chemistry)* denoting the least hydrated acid of a series of oxoacids formed from any one of certain anhydrides, or the anion or a salt formed from such an acid; *Compare* **ortho+** (def. 2), **pyro+** (def. 2). It is now approved only for the polymeric acids: metaboric acid, $(HBO_2)_n$, metaphosphoric acid, $(HPO_3)_n$, and metasilicic acid, $(HSiO_3)_n$; and for anions and salts of these acids (*but see* **metabisulfite**). **3** *(in organic chemistry)* distinguishing a particular polymeric form of the substance named, e.g. metaldehyde, metaformaldehyde.

meta- *symbol*: *m-*; *prefix* (*in organic chemical nomenclature*) denoting the isomer of a disubstituted monocyclic aromatic compound in which the substituents are separated by one intervening unsubstituted ring-carbon atom. *Compare* ***ortho-***, ***para-***.

metabisulfite *an old name, still frequently used, esp. in commerce, for* inorganic salts of the general formula $M_2S_2O_5$, where M is a monovalent metallic element.

metabolic of, pertaining to, occurring in, produced by, or liberated during **metabolism**. —**metabolically** *adv.*

metabolic acidosis any clinical condition in which hydrogen ions accumulate in the blood plasma through an excessive production of acidic metabolites (as in ketoacidosis or lactic acidosis), the excessive ingestion of acids, or a defect in the excretion of hydrogen ions by the kidneys.

metabolic activation **bioactivation**, usually with particular reference to the conversion of procarcinogens to carcinogens in the body.

metabolic alkalosis any clinical condition in which there is a deficiency of hydrogen ions in the blood plasma caused by the excessive ingestion of alkalis, extrarenal loss of acid (as with vomiting), or therapy with diuretic agents.

metabolic balance *see* **balance** (def. 1).

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metabolic block the complete or partial interruption of a specific reaction in a metabolic pathway caused by the absence or greatly reduced activity of the enzyme catalysing that reaction (for genetic reasons or due to the action of a specific agonist). The consequences of a metabolic block include: (1) the complete or partial absence of the final product of the pathway; (2) the accumulation of a metabolic intermediate of the pathway before the block, for which no significant alternative pathway exists; (3) the accumulation of products of an alternative, normally minor, metabolic pathway. *See also* **inborn error of metabolism**.

metabolic code a model for the evolution of biological regulation and the origin of hormone-mediated intercellular communication. It is characterized by a set of symbols and their corresponding domains. A **symbol** is an intracellular molecule, e.g. a hormone or other messenger, that indicates to the cell the existence of a particular state of the environment, e.g. lack of glucose or of amino acids. The symbol regulates a diverse set of biochemical events and reactions in the cell, the nature and number of which are the **domain** of that symbol.

metabolic compartmentation *or* **metabolic compartmentalization** the concept that certain metabolic reactions occur in separate compartments of the cell (or organism) and are therefore not necessarily in equilibrium with each other.

metabolic control *an alternative term for* **metabolic regulation**.

metabolic cycle any closed sequence of metabolic reactions in which an end product is a reactant in the initiation of the cycle, e.g. the **tricarboxylic-acid cycle**.

metabolic disease any disease caused by a recognizable abnormality of metabolism.

metabolic flux the rate of passage of material, or of a specified substance or molecular fragment, through a given metabolic pathway.

metabolic pathway any series of connected (enzymic or other) reactions occurring in a cell or organism, whether anabolic, catabolic, or amphibolic.

metabolic pool the sum total of all the different amounts of a given substance, group of similar substances, or specified molecular fragment, irrespective of their distribution in a cell, organ, tissue, or organism, that are in complete equilibrium with each other in regard to participation in a specified set of metabolic reactions.

metabolic quotient *symbol*: Q_x; a measure of the rate at which a given substance (x) is taken up by, or discharged from, a cell, organ, tissue, or organism.

metabolic rate the rate of metabolism of an animal measured under given conditions. It may be determined from the dioxygen consumption and carbon dioxide (and urinary nitrogen) excretion, or from the total energy output of the animal. *Compare* **basal metabolic rate**.

metabolic regulation the coordinated action of the many systems that control the activity of metabolic pathways. The systems embrace gene regulation and control of protein biosynthesis, as well as the control of the rate of enzyme reactions by phosphorylation of the enzyme protein or by the action of allosteric effectors. The action of second messengers is important in the transduction of signals from outside a cell to the interior.

metabolic state (of mitochondria) *an alternative term for* **respiratory state**.

metabolic turnover the continual exchange of cellular components by degradation and synthesis. Even for cell components for which the content and composition remain relatively constant, a continuous breakdown and resynthesis of individual molecules is occuring.

metabolism **1** the totality of the chemical reactions and physical changes that occur in living organisms, comprising **anabolism** and **catabolism**. **2** the totality of the chemical reactions and physical processes undergone by a particular substance, or class of substances, in a living organism.

metabolite any substance, either endogenous or exogenous, that is formed or changed by metabolism. *See also* **primary metabolite, secondary metabolite**.

metabolize *or* **metabolise** **1** to affect by metabolism. **2** to effect metabolism. —**metabolizable** *or* **metabolisable** *adj.*

metabolon a supramolecular complex of sequential metabolic enzymes and cellular structural elements.

metabotropic describing a type of receptor (e.g. certain **glutamate receptors**) that mediates its effects by activation of enzymes, especially **adenylate cyclase** or the **phosphatidylinositol cycle**, in distinction from receptors that regulate ion channels. *Compare* **ionotropic**. *See also* **excitatory amino-acid receptor**.

metachromasia *or* **metachromasy** *or* **metachromatism** **1** the property exhibited by certain cationic (i.e. basic) dyes of shifting their absorption spectra towards shorter wavelengths in the presence of substances with appropriately arranged anionic groups. **2** the property exhibited by some biological structures or materials, when treated with certain cationic (basic) dyes, of staining with a different colour from that of the dye used. Biological materials showing metachromasia include heparin, chondroitin sulfate, sulfatides, gangliosides, and polyphosphates. —**metachromatic** *adj.*; **metachromatically** *adv.*

metachromatic granule any cytoplasmic granule that exhibits **metachromasia** (def. 2). **Volutin granules** are an example.

metachromatic leukodystrophy any of a group of hereditary diseases of humans characterized by disintegration of myelin and the accumulation of **metachromatic lipid** – galactosyl sulfatide (cerebroside sulfate) – in the white matter of the central nervous system, in peripheral nerves, and in some visceral organs. The accumulation of galactosyl sulfatide is due to deficiency in the activity of **cerebroside sulfatase** (EC 3.1.6.1). The disorder is characterized clinically by progressive paralysis and dementia, usually in the first few years of life, and is transmitted as an autosomal recessive trait. *See also* **saposin**.

metachromism *see* **metachromasia**.

metadrenaline *an alternative name for* **metanephrine**.

metagon a stable, virus-like RNA particle postulated to occur in certain mate-killer strains of *Paramecium aurelia*, in which it acts like messenger RNA.

metahalone any of a class of metaphase inhibitors having the general formula 5-halopyridine-2-one. [From meta(phase) halone.]

metakentrin *an obsolete name for* **luteinizing hormone**.

metal **1** any of a large class of chemical elements that, with certain exceptions, are ductile, malleable solids with a characteristic lustre, are good conductors of electricity and heat, and generally form simple cations. **2** any substance or material consisting entirely or predominantly of one or more **metals** (def. 1). **3** consisting or made of metal. —**metallic** *adj.*

metal-chelate affinity chromatography a method of purifying proteins or other substances that contain, or are dependent on, chelatable metal ions. It consists of a type of **affinity chromatography** in which a chelate-forming adsorbent is used. The adsorbent is prepared by covalently linking molecules of a suitable chelator, e.g. iminodiacetate, via long, stable, hydrophilic spacer arms to a gel-forming matrix, e.g. a preparation of cross-linked agarose, and then saturating it with ions of an appropriate metal, e.g. copper(II); the affinity of the metal ions for the adsorbent must be greater than that for the substance to be separated. Components of a mixture selectively retained by the adsorbent may subsequently be eluted, e.g. with EDTA, by change of pH, or with a gradient of a weak base.

metal-ion buffer a **buffer** (def. 1, 2) for metal ions.

metallo- *comb. form* denoting metal, or characterized by the presence of metal.

metalloantigen any metal-labelled antigen for use in a **metalloimmunoassay**.

metallocarboxypeptidase *recommended generic name for* any **carboxypeptidase** of the sub-subclass EC 3.4.17, for which a bivalent cation is an essential component of the catalytic mechanism.

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metallocene *the generic name for* π-bonded bis(η-cyclopentadienyl) coordination compounds of certain metals, e.g. ferrocene, bis(η-cyclopentadienyl)iron, $[Fe(C_5H_5)_2]$.

metallochromic describing a dye, indicator, or stain that exhibits a distinctive colour change when complexed with metal ions; the colour change is often specific for a particular metal.

metalloendopeptidase *recommended generic name for* any **endopeptidase** of the sub-subclass EC 3.4.24, for which a bivalent cation is an essential part of the catalytic mechanism.

metalloenzyme any enzyme that is a **metalloprotein**.

metallohapten any metal-labelled hapten for use in a **metalloimmunoassay**.

metalloimmunoassay a form of **immunoassay** in which ions of an appropriate transition metal, tightly complexed to the antigen or hapten in question, are used as the distinguishable label. The amount of metal present in the free and antibody-bound forms is determined by a suitable analytical method such as emission, absorption, or fluorescence spectrometry.

metallopeptidase *see* **metallocarboxypeptidase**, **metalloendopeptidase**.

metalloporphyrin any compound formed by chelation of a porphyrin with a metal ion, e.g. hemoglobins (with iron), cytochromes (with iron), and chlorophylls (with magnesium).

metalloprotease *a former name for* metalloendoproteinase (*see also* **metallocarboxypeptidase**, **matrix metalloproteinase**).

metalloprotein any protein containing one or more molecular proportions of a metal bound to it, either directly or as part of a prosthetic group.

metalloproteinase *see* **metallocarboxypeptidase**, **metalloendopeptidase**.

metalloselenonein a synthetic analogue of the copper metallothionein peptide of *Neurospora crassa* that contains selenocysteine residues in place of cysteine.

metallothionein any of a group of very small proteins with extraordinarily high contents both of one or more metals (cadmium, copper, zinc) and of cysteine. They occur widely, from microorganisms to humans, and have highly conserved structures. Mammalian metallothioneins are of 6.8 kDa, consist of 61 amino-acid residues, including 20 cysteine residues, and contain about 7 g atoms of metal per molecule. The apoprotein may be termed **thionein**.

metal proteinase *a former name for* metalloproteinase (*see* **metallocarboxypeptidase**, **metalloendopeptidase**).

metal response element *abbr.*: MRE; a sequence in the promoter region regulating groups of genes that respond to the presence of metals. *See also* **response element**.

metamer *(in chemistry) a former term for* any one of two or more **constitutional isomers** that are of the same chemical class, e.g. ethylamine, $CH_3–CH_2–NH_2$, and dimethylamine, $CH_3–NH–CH_3$.

metamere *(in morphology)* any of the linearly arranged similar body segments in animals that exhibit **metamerism** (def. 2); a somite.

metameric **1** *(in chemistry)* of or pertaining to a **metamer**; pertaining to the phenomenon of, or displaying **metamerism** (def. 1). **2** *(in morphology)* of, or pertaining to, a **metamere**; consisting of metameres; segmented; of, or pertaining to, **metamerism** (def. 2).

metamerism **1** *(in chemistry)* the occurrence as **metamers** of two or more chemical substances of the same molecular formula. **2** *(in morphology)* the condition of an animal body characterized by the presence of a series of similar segments or **metameres**; segmentation.

metameter a quantity derived from an observation, and independent of all parameters, that conveys the magnitude of the phenomenon observed. A metameter is frequently used to simplify the expression or analysis of dose–response relationships.

metamorphosis **1** a complete change in physical form; a structural transformation. **2** *(in zoology)*: the rapid, post-embryonic, structural transformation from a larva into an adult that occurs in certain animals, e.g. the change from a tadpole to a frog. —**metamorphose** *vb.*; **metamorphic** *adj.*

metanephrine *or* **metadrenaline** 3-*O*-methylepinephrine; an inactive metabolite of epinephrine, produced by the action of **catechol *O*-methyltransferase**. Small quantities are normally found in the urine, and larger amounts occur in the urine of patients with catecholamine-secreting tumours.

metaphase the stage in **mitosis**, following **prometaphase**, during which the chromosomes become arranged so that their centromeres all lie in one plane and their longitudinal axes are at right angles to the spindle axis; the corresponding phases in **meiosis**.

metaphosphatase *an alternative name for* **1** endopolyphosphatase (EC 3.6.1.10). **2** exopolyphosphatase (EC 3.6.1.11).

metaphosphate *the traditional name for* any anion or any (partial or full) salt or ester derived from the condensed acid metaphosphoric acid, polytrioxophosphoric(v) acid, $(HPO_3)_n$, where *n* is a small integer, commonly 3, 4, or 6. Metaphosphoric acid and its derivatives are thought not to exist in the monomeric state, although they are often represented as such for convenience. *See also* **polyphosphate**.

metaprotein *an old term for* the products formed by acid or alkaline hydrolysis of proteins that are soluble in weak acids or alkalis but insoluble in neutral solutions.

metarhodopsin either of two intermediates, metarhodopsin I (absorption maximum 480 nm) and metarhodopsin II (absorption maximum 380 nm), formed during the photolysis of **rhodopsin**.

metastable **1** **a** describing any body or system existing in a state of apparent equilibrium when undisturbed, or subject to very small perturbation, but capable of passing to a more stable state when subjected to greater perturbation. **b** describing such a state or such an equilibrium. **2** describing an excited state of an atom, ion, nucleus, or other quantum-mechanical system that is relatively long-lived because the transitions to a lower energy state are forbidden transitions. **3** *symbol*: m; describing any comparatively stable excited state of a radioisotope that decays to a more stable state by isomeric transition, with the emission of gamma radiation, e.g. the metastable nuclide $^{99m}_{43}Tc$, which is formed by decay of $^{99}_{42}Mo$ and which in turn decays by transition to its nuclear isomer $^{99}_{43}Tc$ with a half-life of 6 h and emission of one quantum of gamma radiation.

metastasis (*pl.* **metastases**) the transfer of disease, especially tumour cells, from one part of the body to another by way of the natural passages (blood vessels, lymphatics) or by direct continuity. —**metastasize** *or* **metastasise** *vb.*; **metastatic** *adj.*

metazoa the plural of **metazoan** (def. 1) *or* **metazoon**.

Metazoa a subkingdom of animals consisting of multicellular animals whose cells are organized into tissues and their activities coordinated by a nervous system. The group includes all animals except the Protozoa and Parazoa.

metazoal *a variant form of* **metazoan** (def. 2).

metazoan **1** *or* **metazoon** (*pl.* **metazoa**) any animal of the subkingdom Metazoa. **2** *or* **metazoal** *or* **metazoic** of, characteristic of, or belonging to the Metazoa.

metazoic *a variant form of* **metazoan** (def. 2).

metazoon (*pl.* **metazoa**) *an alternative term for* **metazoan** (def. 1).

[Met^5]enkephalin *or* **[Met]enkephalin** *abbr. for* [5-methionine]enkephalin.

meter **1** an instrument or device for measuring (and recording) the quantity of something (either instantaneously or cumulatively). **2** to measure (something) by means of a **meter** (def. 1). **3** to supply (something) in a measured or regulated amount. **4** *the US spelling of* **metre**.

+meter *comb. form* denoting an instrument or device for measuring (something indicated or specified). —**+metric** *adj.*

metestrus *see* **estrous cycle**.

meth+ *a variant form of* **metho+** *(before a vowel)*.

methadone (hydrochloride) 6-dimethylamino-4,4-diphenyl-3-heptanone hydrochloride; a narcotic analgesic used in cases of opioid dependence.

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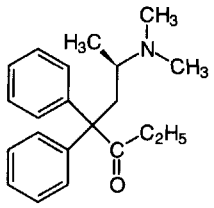


R-(–)-enantiomer

methaemoglobin *a variant spelling (esp. Brit.) of* **methemoglobin**.

methaemoglobinaemia *a variant spelling (esp. Brit.) of* **methemoglobinemia**.

methane *or* **marsh gas** a colourless, odourless, flammable gas, CH_4; it is the simplest alkane and is the principal constituent of natural gas found in association with mineral oil. It is formed by the anaerobic decay of vegetable matter and in large amounts by ruminants and other herbivores.

methano+ *comb. form.* **1** indicating methane. **2** *(in chemical nomenclature)* denoting the presence of a $-CH_2-$ bridge in a polycyclic hydrocarbon.

methanoate *see* **formate**.

methanogen any microorganism that produces methane. —**methanogenic** *adj.*

methanogenesis the microbial production of methane by anaerobic breakdown of carbon-containing compounds.

methanogenic the ability to form methane from CO_2, a property of some anaerobic bacteria. The pathway involves the coenzyme **tetrahydromethanopterin** (*abbr.*: H_4MPT), and involves formation of 5-formyl-H_4MPT, from which successively methenyl-H_4MPT, methylene-H_4MPT, and methyl-H_4MPT are formed in reactions analgous to those for **folate coenzymes**. From the last of these, methyl is transferred to **coenzyme M** to form methyl-coenzyme M, from which methane is formed in a reductive step involving **factor F_{430}**. *See also* **coenzyme F_{420}**.

methanol methyl alcohol; CH_3–OH; the lowest member of the alkanols. It is a colourless, flammable, mobile, poisonous liquid, widely used as a solvent. Numerous esters and ethers of methanol occur naturally, especially in plants. *Other names*: wood alcohol; wood spirit; carbinol. —**methanolic** *adj.*

methanol oxidase *see* **alcohol oxidase**.

methanolysis alcoholysis using methanol.

MetHb *abbr. for* methemoglobin (i.e. **ferrihemoglobin**).

methemoglobin *or (esp. Brit.)* **methaemoglobin** *abbr.*: MetHb; *an older name for* **ferrihemoglobin**.

methemoglobinemia *or (esp. Brit.)* **methaemoglobinaemia** any clinical condition characterized by an excess of **ferrihemoglobin** (i.e. methemoglobin) in the erythrocytes. It accompanies a number of **hemoglobinopathies**, and also results from administration of large amounts of sulfonamides. A hereditary methemoglobinemia is associated with a lack of enzymic capacity to reduce ferrihemoglobin within the red cell. Ferrihemoglobin imparts a brown colour to urine.

methene *an old name, still commonly used in biochemistry, for* the trivalent diatomic group, =CH–, attached to two other groups in an organic molecule. The name now recommended is **methyne**.

methene bridge the **methene** group that links consecutive pyrrole rings in the molecular structure of tetrapyrroles and related compounds.

methenyl+ *prefix (to a trivial biochemical name)* denoting substitution of a **methene** group into the indicated parent compound (at the positions specified by appropriate locants); e.g. 5,10-methenyltetrahydrofolate. *Compare* **methylene+**.

methenyltetrahydrofolate cyclohydrolase EC 3.5.4.9; *systematic name*: 5,10-methenyltetrahydrofolate 5-hydrolase (decyclizing); one of the enzymes involved in transformations between **folate coenzymes**. It catalyses the hydrolysis of 5,10-methenyltetrahydrofolate to form 10-formyltetrahydrofolate. One of three enzymes (*see also* **methylenetetrahydrofolate dehydrogenase (NADP+)** and **formate–tetrahydrofolate ligase**) necessary for the biosynthesis of purines, thymidylate, methionine, histidine, pantothenate, and formyl tRNA-Met. *See* **methylenetetrahydrofolate dehydrogenase (NADP+)** for an example.

5,10-methenyltetrahydrofolate synthetase *see* **5-formyltetrahydrofolate cyclo-ligase**.

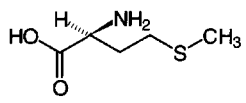
MeTHFA *abbr. for* 5-methyltetrahydrofolate.

methicillin *see* **meticillin (sodium)**.

methine *a former name for* **methyne**.

methioninate **1** methionine anion; the anion, CH_3–S–$[CH_2]_2$–$CH(NH_2)$–COO^-, derived from **methionine**. **2** any salt containing methionine anion. **3** any ester of methionine.

methionine *the trivial name for* α-amino-γ-methylmercaptobutyric acid; 2-amino-4-(methylthio)butanoic acid; CH_3–S–$[CH_2]_2$–$CH(NH_2)$–COOH; a chiral α-amino acid. L-Methionine (*symbol*: M *or* Met), (*S*)-2-amino-4-(methylthio)butanoic acid, is a coded amino acid, found in peptide linkage in proteins; codon: AUG (or AUA also in various species of mitochondria). D-Methionine (*symbol*: D-Met *or* DMet) is not known to occur naturally. In mammals methionine is glucogenic and is an essential dietary amino acid, although either enantiomer will serve (the D-form being oxidatively deaminated to the α-oxo acid, which is then reaminated with inversion).



L-methionine

methionine adenosyltransferase EC 2.5.1.6; *other names*: *S*-adenosylmethionine synthetase; AdoMet synthetase; an enzyme that catalyses the formation of *S*-adenosyl-L-methionine from L-methionine, ATP, and H_2O with the release of pyrophosphate and orthophosphate. Example from *Escherichia coli*: database code METK_ECOLI, 384 amino acids (42.03 kDa). Example from human: database code METK_HUMAN, 395 amino acids (43.61 kDa).

methionine dioxide *symbol*: $MetO_2$; methionine *S*,*S*-dioxide; CH_3–SO_2–$[CH_2]_2$–$CH(NH_2)$–COOH; an oxidation product of methionine, *formerly known (incorrectly) as* **methionine sulfone**.

[5-methionine]enkephalin *abbr.*: [Met]enkephalin *or* [Met^5]enkephalin; the recommended designation for the trivial name of the pentapeptide Tyr-Gly-Gly-Phe-Met. *See* **enkephalin**.

methionine oxide *symbol*: MetO; methionine *S*-oxide; CH_3–SO–$[CH_2]_2$–$CH(NH_2)$–COOH; an oxidation product of methionine and an intermediate in the formation of **methionine dioxide**. *It was formerly known (incorrectly) as* **methionine sulfoxide**.

methionine salvage pathway a metabolic cycle in which methionine is synthesized from carbons originating in the ribose of ATP, the sulfur atom being conserved throughout the cycle. In outline, the cycle consists of reactions in which, starting with L-methionine, ***S*-adenosylmethionine** (I) is formed in a reaction with ATP. I is then converted by 1-aminocyclopropane-1-carboxylate synthase, EC 4.4.1.14, to 5′-methylthioadenosine (II) and 1-aminocyclopropane-1-carboxylate, a precursor of ethylene (*see* **ethylene-forming enzyme**). Adenine is then cleaved from methylthioadenosine to form 5-methylthioribose from which 5-methylthioribose-1-phosphate (III) is formed by reaction with ATP. III is then converted through a series of intermediates to 2-keto-4-methylthiobutyrate from which methionine is formed by a transamination reaction.

methionine sulfone *an old (incorrect) name for* **methionine dioxide**.

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methionine sulfoxide *an old (incorrect) name for* **methionine oxide**.

methionine sulfoximine [3-amino-3-carboxypropyl]methyl sulfoximine; an inhibitor of glutamine synthetase (**glutamate–ammonia ligase**) in plants, and identified as the toxic agent in flour treated with the bleaching agent NCl_3 (agene, hence the term **agenized flour**). It interferes with the action of γ-amino-*n*-butyric acid in the brain. This is associated with the ability of methionine sulfoximine to cause fits in a wide variety of animals – ferrets are particularly susceptible. Although methionine sulfoximine has not been clearly proven to be toxic to humans, agene is no longer used for bleaching flour.

methionine synthase *see* **homocysteine methyltransferase**.

methioninium methionine cation; the cation, $CH_3–S–[CH_2]_2–CH(NH_3^+)–COOH$, derived from **methionine**.

methionino the alkylamino group, $CH_3–S–[CH_2]_2–CH(COOH)–NH–$, derived from **methionine**.

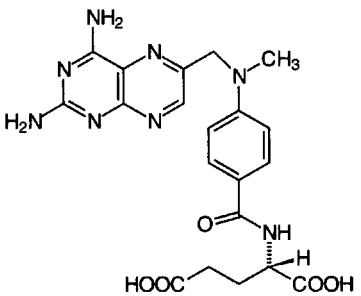
methionyl the acyl group, $CH_3–S–[CH_2]_2–CH(NH_2)–CO–$, derived from **methionine**.

methionyllysylbradykinin *or* **Met-Lys-bradykinin** *see* **bradykinin**.

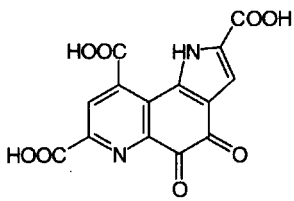
methionyl-tRNA formyltransferase EC 2.1.2.9; *systematic name*: 10-formyltetrahydrofolate:L-methionyl-tRNA *N*-formyltransferase. An enzyme that catalyses a reaction between 10-formyltetrahydrofolate, L-methionyl-tRNA, and H_2O to form tetrahydrofolate and *N*-formylmethionyl-tRNA. *N*-formylmethionyl-tRNA is involved in the initiation of prokaryote **translation**. Example from *Escherichia coli*: database code FMT_ECOLI, 314 amino acids (34.00 kDa).

metho+ *or (before a vowel)* **meth+** *(comb. form) a variant of* **methyl+** in the names of certain chemical compounds.

methotrexate 4-amino-10-methylfolic acid; *other name*: amethopterin; a folic acid analogue that is a potent competitive inhibitor ($K_i < 10^{-9}$ M) of **dihydrofolate reductase**. It is useful as an antineoplastic agent in the treatment of acute leukemia and choriocarcinoma. It acts by blocking nucleotide synthesis and thus also DNA synthesis and has similar activity to **aminopterin**. The structure of a complex of methotrexate and dihydrofolate reductase from *Lactobacillus casei* is known: database code NRL_3DFR.



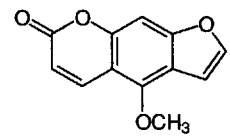
methoxatin *or* **pyrroloquinoline quinone** 4,5-dihydro-4,5-dioxo-1*H*-pyrrolo-[2,3-*f*]quinoline-2,7,9-tricarboxylic acid; a heat-stable fluorescent cofactor implicated in the action of primary alcohol dehydrogenases in methylotrophic bacteria and possibly more generally associated with the oxidation of single-carbon compounds.



methoxy *symbol*: OMe *or* MeO; the alkoxy group, $CH_3–O–$, derived from methanol by loss of a hydrogen atom.

3-methoxy-4-hydroxymandelate acid *See* **hydroxymethoxymandelate**.

5-methoxypsoralen an intercalating reagent for DNA; it forms covalent cross-links on irradiation. *See also* **psoralen**.



methoxyvinylglycine *abbr.*: MVG; L-2-amino-4-methoxy-*trans*-3-butenoic acid; an inhibitor of ethylene biosynthesis in plants.

methyl *symbol*: Me; the alkyl group, $CH_3–$, derived from methane.

methyl- *prefix (in chemical nomenclature)* used as a locant to indicate in or at a methyl group.

methyl-accepting chemotaxis protein *abbr.*: MCP; any of several similar integral plasma membrane proteins, one or more of which may be present in the cell membranes of particular strains of certain motile bacteria, e.g. *Escherichia coli* and *Salmonella typhimurium*, and each of which appears to mediate the responses of these organisms to corresponding classes of chemotactic agent by undergoing enzymic methylation/demethylation of the γ-carboxylate group(s) of one or more glutamic residues (for the enzymes responsible *see* ***che***). The type of ligand determines the nature of the methylation, which in turn determines the action of the receptor on the bacterial flagellar motor, so that the effect can be either attractant or repellent. The following examples are from *E. coli*. MCP1 is a receptor for attractants such as L-serine and other amino acids and is also responsible for chemotaxis away from a wide range of repellents, including leucine, indole, and weak acids; database code MCP1_ECOLI, 551 amino acids (59.38 kDa). MCP2 is a receptor for L-aspartate, dicarboxylic acids, and maltose (via interaction with a periplasmic maltose-binding protein), and is also responsible for chemotaxis away from cobalt and nickel; database code MCP2_ECOLI, 553 amino acids (59.96 kDa). MCP3 interacts with periplasmic ribose- or galactose-binding proteins and mediates taxis towards these sugars; database code MCP3_ECOLI, 535 amino acids (57.99 kDa). MCP4 interacts with periplasmic dipeptide-binding proteins and mediates taxis towards such peptides; database code MCP4_ECOLI, 535 amino acids (57.65 kDa).

***N*^{6}-methyladenine** a methylated base of DNA; this and **5-methylcytosine** are the only modified bases in the DNA of cellular organisms.

methyl alcohol *a common name for* **methanol**.

methylase *a common name for* **methyltransferase**.

methylaspartase *see under* **methylaspartate mutase**.

***N*-methyl-D-aspartate** *abbr.*: NMDA; an excitatory amino acid and a neurotransmitter. It acts as agonist for the *N*-methyl-D-aspartate receptor, a subclass of glutamate ionotropic receptors (*see* **glutamate receptor**).

methylaspartate ammonia-lyase *recommended name for* methylaspartase; *see under* **methylaspartate mutase**.

methylaspartate mutase EC 5.4.99.1; *systematic name*: L-*threo*-3-methylaspartate carboxy-aminomethylmutase; *other name*: glutamate mutase. An enzyme that catalyses the reaction:

L-*threo*-3-methylaspartate = L-glutamate.

This is the first step of the glutamate-fermentation pathway of the anaerobic bacteria *Clostridium cochlearium*, *C. tetanomor-*

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phum, and others. The product, (2*S*, 3*S*)-3-methylaspartate, is converted to mesaconate by the enzyme methylaspartate ammonia-lyase (EC 4.3.1.2). Methylaspartate mutase requires a cobamide coenzyme and has been studied as an example of such a reaction. The enzyme has two subunits (large and small, sometimes called E and S). Examples from *C. tetanomorphum*: large chain, database code S32433, 485 amino acids (53.68 kDa); small chain, database code S29502, 137 amino acids (14.73 kDa).

methylate 1 to introduce (one or more) methyl groups into (a substance). 2 *(in commerce)* to mix or adulterate with methanol. —**methylation** *n.* *See also* **methylation of DNA**.

methylated-DNA–protein-cysteine *S*-methyltransferase EC 2.1.1.63; *other names*: 6-*O*-methylguanine-DNA methyltransferase; O^6-methylguanine-DNA-alkyltransferase. It catalyses the reaction between DNA (containing 6-*O*-methylguanine) and protein L-cysteine to form DNA (without 6-*O*-methylguanine) and protein *S*-methyl-L-cysteine. As the acceptor is in the enzyme itself this is a 'suicidal' reaction. Bacterial and mammalian enzymes have common motifs. Example from *Escherichia coli*: database code OGT_ECOLI, 171 amino acids (19.06 kDa).

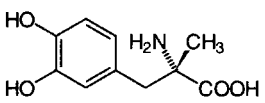
methylation of DNA the occurrence in vertebrate DNA of varying amounts of 5-methylcytosine which arises from methylation of cytosine bases where they occur in the sequence CpG. The methylation status of DNA correlates with its functional activity: inactive genes are more heavily methylated. *See also* **CpG islands**.

3-methylcholanthrene a carcinogenic hydrocarbon, found in coal tar. It induces synthesis of cytochrome P450 mRNA.

methylcrotonyl-CoA carboxylase EC 6.4.1.4; an enzyme of the pathway for the degradation of leucine. It catalyses the formation of 3-methylglutaconyl-CoA from ATP, 3-methylcrotonyl-CoA, and HCO_3^- with release of ADP and orthophosphate. Biotin is a cofactor. The 3-methylglutaconyl-CoA is then converted to 3-hydroxy-3-methylglutaryl-CoA.

5-methylcytosine a methylated base of DNA; this and ***N*^{6}-methyladenine** are the only modified bases in the DNA of cellular organisms. In T-even phages all the C residues of DNA are 5-hydroxymethylcytosine.

methyldopa L-2-amino-2-methyl-3-(3,4-dihydroxyphenyl)propionic acid; a compound used as an antihypertensive. It is a competitive inhibitor of **aromatic L-amino acid decarboxylase** (dopa decarboxylase), but its effects on blood pressure may result from its metabolism to α-methylnorepinephrine which stimulates presynaptic α_2 receptors, thus decreasing norepinephrine release.



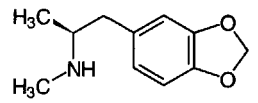
methylene 1 *the recommended name for* the bivalent triatomic group CH_2 in a molecule, whether attached to two other atoms by single bonds or to one other atom by a double bond. 2 *a former name for* **carbene** (def. 1).

methylene+ *prefix (to a trivial chemical name)* denoting substitution of a **methylene** group into the indicated parent compound (at the positions specified by appropriate locants); e.g. 5,10-methylenetetrahydrofolate (which may be shortened to 5,10-CH_2-H_4folate). *Compare* **methenyl+**.

***N*,*N*′-methylenebisacrylamide** $(CH_2{:}CHCONH_2)_2CH_2$; a cross-linking agent used in a ratio (w/w) of between 1:49 and 1:19 with acrylamide in the preparation of polyacrylamide gels.

Methylene Blue *or* **Swiss Blue** *or* **Basic Blue 9** CI 52015; tetramethylthionine chloride; 3,7-bis(dimethylamino)phenothiazinium chloride; a water- and ethanol-soluble blue dye; A_{max} (in water) at 663–667 nm. It is reducible to a leuko (i.e. colourless) compound, which is reoxidizable by dioxygen, and hence is useful as a redox indicator; $E^{o\prime}$ (pH 7.0, 30 °C) = +0.011 V. It is useful also as a stain in bacteriology and histology, e.g. being preferentially taken up by melanin-containing cells and can be used to target therapeutic agents to such cells.

3,4-methylenedioxymethamphetamine *abbr.*: MDMA; a phenethylamine derivative and analogue of **mescaline** and **amphetamine** that is a potent CNS stimulant and hallucinogen; *popularly known as* **ecstasy**. A controlled substance in the US Code of Federal Regulations.



S-(+)-enantiomer

2-methyleneglutarate mutase EC 5.4.99.4; *systematic name*: 2-methyleneglutarate carboxy-methylenemethylmutase. An enzyme that catalyses the reaction:

2-methyleneglutarate = 2-methylene-3-methylsuccinate.

It is a key enzyme in the fermentation of nicotinate to ammonia, propionate, acetate, and CO_2 by the strict anaerobe *Clostridium barkeri*, but has been much investigated as an example of an enzyme mechanism based on the adenosylcobalamin coenzyme. 2-Methylene-3-methylsuccinate is converted to 2,3-dimethylmaleate by methylitaconate Δ-isomerase (EC 5.3.3.6). The enzyme is a homotetramer of 70 kDa subunits: database code CBMGM1, 614 amino acids (66.67 kDa).

methylene-interrupted double bonds double bonds separated by one methylene group. The term is used especially to describe the double bonds in naturally occurring long-chain fatty acids; in many cases these are all of the *Z* configuration, with each pair separated by one methylene group.

methylenetetrahydrofolate dehydrogenase (NADP$^+$) EC 1.5.1.5; *systematic name*: 5,10-methylenetetrahydrofolate: $NADP^+$ oxidoreductase. *other name*: C1-tetrahydrofolate synthase, cytoplasmic; an enzyme involved in the interconversion of folate coenzymes that catalyses the reaction:

5,10-methylenetetrahydrofolate + $NADP^+$ =
5,10-methenyltetrahydrofolate + NADPH.

One of three enzymes (*see also* **methenyltetrahydrofolate cyclohydrolase**, and **formate–tetrahydrofolate ligase**) necessary for the biosynthesis of purines, thymidylate, methionine, histidine, pantothenate, and formyl tRNA-Met. Example from human, a cytoplasmic trifunctional homodimer: database code C1TC_HUMAN, 934 amino acids (101.31 kDa) – this has an N-terminal domain (amino acids 1–304) with methylenetetrahydrofolate dehydrogenase and cyclohydrolase activity; the C-terminal section (305–934) forms the formyltetrahydrofolate synthetase domain; *other names*: mitochondrial (precursor) NAD-dependent methylenetetrahydrofolate dehydrogenase (EC 1.5.1.5)/methenyltetrahydrofolate cyclohydrolase (EC 3.5.4.9): database code MTDC_HUMAN, 344 amino acids (37.28 kDa).

5,10-methylenetetrahydrofolate reductase (FADH$_2$) EC 1.7.99.5; an enzyme that catalyses the reaction:

5-methyltetrahydrofolate + acceptor =
5,10-methylenetetrahydrofolate + reduced acceptor.

FAD is a coenzyme. Example from *Escherichia coli*: database code METF_ECOLI, 296 amino acids (33.06 kDa).

methylesterase any of various enzymes that catalyse the hydrolysis of methyl esters. For example, **juvenile-hormone esterase** (EC 3.1.1.59) of insects, *other name*: JH-esterase,

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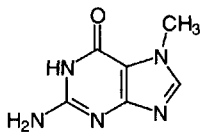
catalyses the hydrolysis of methyl (2*E*,6*E*)-(10*R*,11*S*)-10,11-epoxy-3,7,11-trimethyltrideca-2,6-dienoate to form (2*E*,6*E*)-(10*R*,11*S*)-10,11-epoxy-3,7,11-trimethyltrideca-2,6-dienoate and methanol; i.e. it demethylates the insect juvenile hormones JH_1 and JH_2. Example (precursor) from the moth *Heliothis virescens*: database code ESTJ_HELVI, 564 amino acids (62.53 kDa); it is similar to certain other carboxylesterases and lipases. Another example, the **protein-glutamate methylesterase** of *Escherichia coli*, is involved in chemotaxis in this organism (*see* ***che***).

methylglucosamine *N*-methyl-L-glucosamine; 2-deoxy-2-(methylamino)-L-glucose; a component of **streptomycin**.

***O*^{6}-methylguanine** a modified and, in principle, highly mutagenic base in DNA (it base pairs with T). It has a special detoxication enzyme, **methylated-DNA–protein-cysteine *S*-methyltransferase**.

7-methylguanine a modified base found in transfer RNA. *See* **guanine** (for numbering), **7-methylguanosine**.



7-methylguanosine a modified nucleoside that forms a **cap** at the 5′-terminus of eukaryotic mRNA. *See also* **7-methylguanine**.

methylidyne *the recommended name for* the trivalent diatomic group CH≡ attached to a single other group in a molecule of an organic compound. *Compare* **methine**.

methylmalonate $CH_3CH(COO^-)_2$; isosuccinate 2-methylpropanedioate; the dianion of methylmalonic acid; as **methylmalonyl-CoA** it is an intermediate in the conversion of propionyl-CoA to succinyl-CoA. Note: methylmalonate should be distinguished from methyl malonate (two words), which is propanedioic acid dimethyl ester.

methylmalonic acidemia *or* **methylmalonic aciduria** any of a group of diseases, inherited as autosomal recessive traits, in which abnormally large amounts of methylmalonate occur in the blood and urine. The condition may be caused by abnormalities in either **methylmalonyl-CoA epimerase** or **methylmalonyl-CoA mutase** apoenzymes, or by three different abnormalities in adenosylcobalamin synthesis.

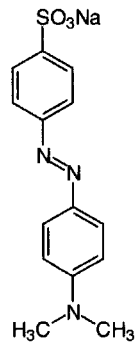
methylmalonyl-CoA 2-carboxypropanoyl-CoA; it can exist as the enantioners (*R*)- and (*S*)-methylmalonyl-CoA; (*S*)-methylmalonyl-CoA is an intermediate in the **beta oxidation** of odd-numbered fatty acids in animals. Propionyl-CoA is the major end product; for further metabolism, this is converted to succinyl-CoA by, first, carboxylation to (*S*)-methylmalonyl-CoA, which is converted by **methylmalonyl-CoA epimerase** to (*R*)-methylmalonyl-CoA, which is then converted to succinyl-CoA by **methylmalonyl-CoA mutase**.

methylmalonyl-CoA epimerase EC 5.1.99.1; an enzyme that interconverts (*R*)methylmalonyl-CoA to (*S*)-methylmalonyl-CoA. It is sometimes incorrectly referred to as methylmalonyl-CoA racemase (chiral centres in the CoA moiety are not affected).

methylmalonyl-CoA mutase EC 5.4.99.2; *systematic name*: (*R*)-2-methyl-3-oxopropanoyl-CoA CoA-carbonylmutase; an enzyme that converts (*R*)-methylmalonyl-CoA to succinyl-CoA; adenosylcobalamin is a cofactor. Example from human, homodimer (precursor): database code MUTA_HUMAN, 750 amino acids (83.01 kDa). This enzyme is required for degradation of several amino acids, odd-chain fatty acids, and cholesterol via propionyl-CoA to the tricarboxylic-acid cycle; deficiency results in **methylmalonic acidemia**. It is a mitochondrial enzyme (the precursor includes a transit peptide in amino acids 1–32). In some bacteria the enzyme is a heterodimer; both subunits have homology with the human protein. The metabolic role is in the synthesis of propionate from tricarboxylic-acid-cycle intermediates. Examples from *Propionobacter freudenreichii shermanii*, α subunit: database code MUTA_PROFR, 638 amino acids (69.39 kDa); β subunit: database code MUTB_PROFR, 728 amino acids (80.09 kDa).

2-methyl-1,4-naphthalenedione 2-methyl-1,4-naphthoquinone; *see* **menadione**.

Methyl Orange a dye used as an indicator, changing from red to orange-yellow over the pH range 3.1–4.4.



methylotroph any organism that can use certain single-carbon compounds, in a lower oxidation state than CO_2, as sole carbon source. —**methylotrophic** *adj.*; **methylotrophy** *n.*

methylotrophic yeast any yeast belonging to either of the genera *Hansenula* or *Pichia*. They are potentially valuable recombinant-DNA expression hosts as certain oxidase genes (*MOX* and *AOX*) are vastly overexpressed and their promoters are suitable for the expression of foreign proteins. *See also* **alcohol oxidase**, **methylotroph**.

3-methyl-2-oxobutanoate dehydrogenase (lipoamide) EC 1.2.4.4; *other names*: 2-oxoisovalerate dehydrogenase; branched-chain α-keto-acid dehydrogenase; branched-chain α-keto-acid decarboxylase; an enzyme activity present in a complex that catalyses the oxidative decarboxylation of oxo acids derived from branched-chain amino acids. It is similar in mechanism to the **pyruvate dehydrogenase complex**. This enzyme is the E_1 component of the complex, and catalyses the release of CO_2 from the oxo acid and transfer of the resulting acyl group to lipoamide. Thus, for the oxo acid from valine, it catalyses the reaction of 3-methyl-2-oxobutanoate with lipoamide to form *S*-(2-methylpropanoyl)dihydrolipoamide with release of CO_2. Thiamine diphosphate is a coenzyme. Example from human, precursors of α and β subunits respectively: database codes ODBA_HUMAN, 445 amino acids (50.41 kDa); ODBB_HUMAN, 392 amino acids (43.07 kDa). *See also* **[3-methyl-2-oxobutanoate dehydrogenase (lipoamide)] kinase**.

[3-methyl-2-oxobutanoate dehydrogenase (lipoamide)] kinase EC 2.7.1.115; *other name*: branched-chain α-keto-acid dehydrogenase kinase; an enzyme that catalyses the phosphorylation by ATP of [3-methyl-2-oxobutanoate dehydrogenase (lipoamide)] with release of ADP, thereby inactivating the enzyme complex. Example (precursor) from rat: database code BCKD_RAT, 412 amino acids (46.34 kDa).

[3-methyl-2-oxobutanoate dehydrogenase (lipoamide)]-phosphatase EC 3.1.3.52; *other name*: branched-chain oxo-acid dehydrogenase phosphatase; an enzyme that catalyses the hydrolysis of phosphate from [3-methyl-2-oxobutanoate dehydrogenase (lipoamide)] phosphate.

Methyl Red a dye used as an indicator, changing from red to yellow over the pH range 4.2–6.3. (Illustrated on p. 414.)

methylsulfonyl nitrophenyl carbonate 2-(methylsulfonyl)-ethyl 4-nitrophenyl carbonate; a reagent used for the introduction of the **MSOC** amino-protecting group.

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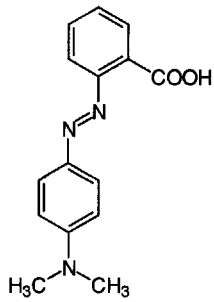
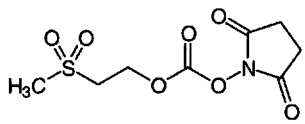
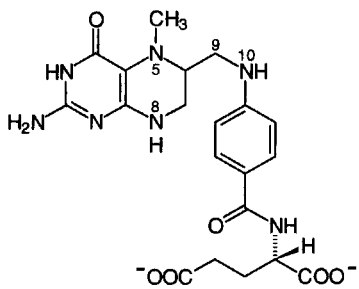


Methyl Red

methylsulfonyl succinimidyl carbonate 2-(methylsulfonyl)-ethyl *N*-succinimidyl carbonate; a reagent used for the introduction of the **MSOC** amino-protecting group.



5-methyltetrahydrofolate *abbr.*: MeTHFA *or* 5-CH_3-H_4folate; a member of the tetrahydrofolate group of coenzymes. One of its functions is to act as intermediate in the methylation of vitamin B_{12}, which can then react with homocysteine to form methionine. The methyl group of MeTHFA is derived from C-3 of serine via 5,10-methylene H_4folate.

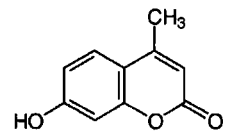


methyltetrahydrofolate trap hypothesis a hypothesis to explain the accumulation of 5-methyltetrahydrofolate (5-CH_3-H_4folate) in the sera of patients with vitamin B_{12} deficiency. It suggests that, because the only route by which 5-CH_3-H_4folate can be converted to H_4folate (required for single-carbon transfer reactions) is by the vitamin B_{12}-dependent 5-methyltetrahydrofolate–homocysteine *S*-methyltransferase (EC 2.1.1.13) reaction, a large proportion of the body's available folate becomes trapped as 5-CH_3-H_4folate, leading to folate deprivation.

methylthioribose 5-methylthio-D-ribose; an intermediate in the **methionine salvage pathway**.

methyltransferase any of the enzymes of sub-subclass EC 2.1.1, which catalyse the transfer of a methyl group. *See also* ***che***, ***O*^{6}-methylguanine**.

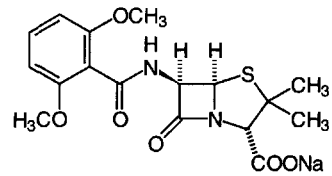
4-methylumbelliferyl *abbr.*: MU; a group that is attached in glycosidic linkage to various sugars to form substrates useful in the assay of glycosidases. The highly fluorescent 4-methylumbelliferone is released on enzyme action, and can be measured in alkaline solution by its fluorescence (max. 448 nm, excitation at 364 nm), which is quenched in the glycosidic substrate. *See also* **MUG**.



4-methylumbelliferone

methyne *or (formerly)* **methine** *the name now recommended for* the trivalent diatomic group, =CH–, attached to two other groups in an organic molecule. Such a group is commonly still known in biochemistry as **methene**. *Compare* **methylidyne**.

meticillin (sodium) *or* **methicillin** a semisynthetic antibiotic of the **penicillin** type that is lactamase resistant.



metJ the gene for the repressor (co-repressor is *S*-adenosylmethionine) of the methionine biosynthetic operon, and also *metJ* itself, in *Escherichia coli*. The repressor protein undergoes dimeric binding to DNA by a motif other than a helix-turn-helix. Database code METJ_ECOLI, 104 amino acids (12.00 kDa).

Met-Lys-bradykinin *a short name for* methionyllysylbradykinin; *see* **bradykinin**.

MetMb *abbr. for* metmyoglobin (i.e. **ferrimyoglobin**).

metmyoglobin *abbr.*: MetMb; *an old name for* **ferrimyoglobin**.

metre *or (US)* **meter** *symbol*: m; the SI base unit of length, equal to the length of the path travelled by light in a vacuum during a time interval of 1/299 792 458 of a second.

metre–kilogram–second system (of electrical units) *abbr.*: mks system *or* MKS system; a system of electrical (physical) units based on the metre, kilogram, and second as fundamental units of measurement. It has now been superseded by the **SI** system of units.

metric **1** of, or relating to, the metre or the metric system. **2** quantitative.

+metric *see* **+meter**, **+metry**.

metric system a system of weights and measures, devised in France (1793–95), based on the principle that each of the physical quantities length, volume, and mass should be defined in terms of one unit whose multiples and submultiples are related by powers of ten and that all three units should be simply interrelated. The units were, respectively, the metre, the litre (one cubic decimetre), and the gram (the mass of one cubic centimetre of water at its maximum density). It has now been supplanted by the International System of Units (*see* **SI**).

metridin **1** a toxin from *Metridium senile* (brown sea anemone); database code TXAM_METSE, 36 amino acids (3.97 kDa). **2** *or* **metridium proteinase A** EC 3.4.21.3; *other name*: sea anemone protease A; an enzyme that catalyses the preferential cleavage: Tyr-|-Xaa > Phe-|-Xaa > Leu-|-Xaa; it has little action on Trp-|-Xaa.

metridium proteinase A *see* **metridin** (def. 2).

metrizamide *the trivial name for* 2-[3-acetamido-5-(*N*-methylacetamido)-2,4,6-triiodobenzamido]-2-deoxy-D-glucose; a dense,

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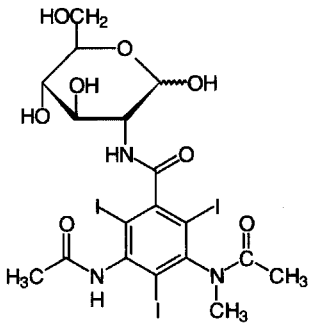
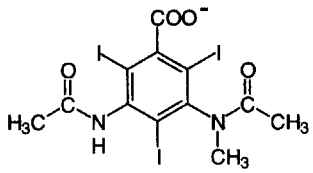
synthetic, nonionic substance, highly soluble in water, that is capable of forming (nonautoclavable) aqueous solutions of densities up to 1.3 g cm^{-3}, useful as media for **isopycnic centrifugation** of biological particles.

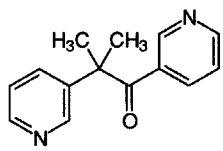


metrizoate *the trivial name for* the 3-acetamido-5-(*N*-methylacetamido)-2,4,6-triiodobenzoate anion; a dense, synthetic substance used primarily as its sodium salt, which is highly soluble in water and capable of forming autoclavable aqueous solutions of densities up to 1.4 g cm^{-3}, or more, such solutions being useful as media for **isopycnic centrifugation** of biological particles.



+metry *comb. form* denoting the process or science of measuring (something indicated or specified). —**+metric** *adj.*

metyrapone 2-methyl-1,2-di(3-pyridyl)propan-1-one; an inhibitor of the enzyme 11β-hydroxylase (steroid 11β-monooxygenase; EC 1.14.15.4); this enzyme is involved in the synthesis of cortisone, cortisol and aldosterone, its inhibition causing a rise in **corticotropin** secretion as a result of release from negative feedback on the pituitary by cortisol. Metyrapone is used in **challenge** tests of hypothalamic-pituitary function and sometimes in the treatment of **Cushing's syndrome**.

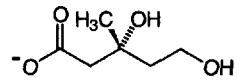


MeV *symbol for* megaelectronvolt (i.e. 10^6 electronvolts).

Mevacor *a proprietary name for* **lovastatin**.

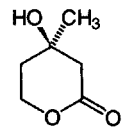
mevaldate **1** the anion OHC–CH_2–$C(CH_3)$(OH)–CH_2–COO^- derived from mevaldic acid; its (*R*)-enantiomer occurs as an enzyme-bound intermediate during the conversion of hydroxymethylglutaryl-coenzyme A to mevalonate in the biosynthesis of polyprenyl compounds. **2** any salt or ester of mevaldic acid.

mevalonate **1** the anion, HO–$[CH_2]_2$–$C(CH_3)$(OH)–CH_2–COO^-, derived from mevalonic acid; its (*R*)-enantiomer is a strategic intermediate derived from hydroxymethylglutaryl-CoA in the biosynthesis of polyprenyl compounds. **2** any salt or ester of mevalonic acid.



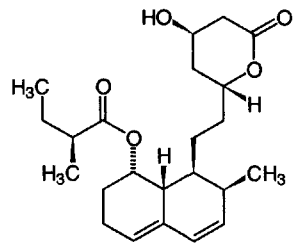
(*R*)-mevalonate

mevalonolactone mevalonic acid lactone; it is hydrolysed in cells to mevalonate, and is often the form in which mevalonate is administered to animals or cells, either radioaactively or non-radioactively as a metabolic precursor.



mevalonoyl the acyl group, HO–$[CH_2]_2$–$C(CH_3)$(OH)–CH_2–CO–, derived from mevalonic acid.

mevastatin *or* **compactin** 6-demethylmevinolin; a substance isolated from *Penicillium citrinum*; it is a potent inhibitor of **HMG-CoA reductase** with actions similar to **lovastatin**.



Mevinacor *a proprietary name for* **lovastatin**.

mevinolin *an alternative name for* **lovastatin**.

Meyerhof, Otto Fritz (1884–1951), German physiologist and biochemist; Nobel Laureate in Physiology or Medicine (1922) 'for his discovery of the fixed relationship between the consumption of oxygen and the metabolism of lactic acid in the muscle' [prize shared with A. V. Hill].

Meyerhof pathway *see* **Embden–Meyerhof pathway**.

Meyerhof quotient an index of the effect of the presence or absence of dioxygen on glycolysis or fermentation. It is: [(rate of anaerobic fermentation) – (rate of aerobic fermentation)]/(rate of dioxygen uptake). Assuming 6 mol ATP are formed per mol dioxygen used, a Meyerhof quotient of 6 would mean that aerobic and anaerobic energy supply are the same; a lower value indicates an increase in ATP-supplying and ATP-requiring processes on transition from anaerobic to aerobic conditions.

mfd *abbr. for* microfarad.

mg *symbol for* milligram (i.e. 10^{-3} gram).

Mg *symbol for* magnesium.

MHC *abbr. for* major histocompatibility complex.

mho a practical unit of electric conductance equal to the reciprocal of the impedance measured in ohms. For circuits containing only noninductive resistance the **siemens** is the preferred unit.

MHS *abbr. for* major histocompatibility system (i.e. **major histocompatibility complex**).

MIC *abbr. for* minimum inhibitory concentration.

mica substrate technique a technique used in preparing

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specimens of macromolecules for electron microscopic examination. Freshly cleaved mica is used to support the specimen during shadowing with a metal; a backing film of carbon is then applied by evaporation normal to the shadowed surface, and both films are transferred to the grid.

micelle **1** an aggregate, of colloidal dimensions, of oriented molecules of amphipathic substances existing in equilibrium in solution with the chemical species from which it is formed; micelles are generally electrically charged. In aqueous solution the individual molecules of the micellar aggregate are oriented with their polar groups pointing towards the aqueous medium and their hydrophobic moiety directed into the centre of the micelle. **2** a hypothetical ordered region in a natural fibre such as cellulose. —**micellar** *adj.*

micellization *or* **micellisation** transformation into micelles.

micF a regulatory gene in the osmoregulatory system in *Escherichia coli*; *micF* RNA and *ompF* mRNA (omp = outer membrane protein) are induced by interaction of *ompR* with a common divergent, central promoter region. *micF* RNA is partly complementary to the Shine–Dalgarno region of *ompC* and thus represses its expression by translational control.

Michaelian of, relating to, or described by **Michaelis kinetics**.

Michaelis, Leonor (1875–1949), German physician and biochemist; distinguished for his contributions to the theory of hydrogen ions and to the development of the theory of enzyme–substrate combination. He also worked in Japan and latterly in the USA.

Michaelis kinetics *or* **Michaelis–Menten kinetics** a model to explain the kinetics of an enzyme-catalysed reaction,

$$E + S \underset{k_{-1}}{\overset{k_{+1}}{\rightleftharpoons}} ES \xrightarrow{k_{cat}} E + P$$

where E is enzyme, S is substrate, ES is an intermediate complex (the **Michaelis complex**), and P is product. The initial velocity of the reaction, v, when [P] = 0, is given by the **Michaelis equation** (or **Michaelis–Menten equation**):

$$v = V[S]/(K_m + [S]) = d[P]/dt$$

in which V is the limiting or maximal reaction rate (i.e. that occurring when the enzyme is saturated with substrate), and the **Michaelis constant**, K_m, is given by:

$$K_m = (k_{-1} + k_{cat})/k_{+1}.$$

If $k_{cat} << k_{+1}$, then K_m approximates to K_s, the enzyme–substrate dissociation constant (usually known as the **substrate dissociation constant**). K_m and V are known as the **Michaelis parameters**. *Compare* **Dalziel coefficient**.

Michaelis pH function any one of a set of functions relating hydron concentration, $[H^+]$, to the acid dissociation constants for different stages of dissociation of a given polybasic acid.

Consider first the simplest example, that of a symmetrical dibasic acid, AH_2 (e.g. succinic acid). This can exist in three stages of dissociation, represented by the equilibria

$$AH_2 \underset{}{\overset{K_1}{\rightleftharpoons}} AH^- \overset{K_2}{\rightleftharpoons} A^{2-}$$

where K_1 and K_2 are the acid dissociation constants for the respective stages of dissociation. For such a dissociation there are three Michaelis pH functions, f_0, f_1, and f_2, which are defined thus:

$$f_0 = 1 + K_1/[H^+] + K_1K_2/[H^+]^2$$

$$f_1 = 1 + [H^+]/K_1 + K_2/[H^+]$$

$$f_2 = 1 + [H^+]/K_2 + [H^+]^2/K_1K_2$$

The total concentration of acid of all forms, $[A]_t$, is given by

$$[A]_t = [AH_2] + [AH^-] + [A^{2-}];$$

by substitution for K_1 and K_2 it can be shown that

$$[A]_t = f_0[AH_2] = f_1[AH^-] = f_2[A^{2-}]$$

Hence it will be apparent that the reciprocals of the respective pH functions give the fractional concentrations of the various ionic forms of the acid at a given pH value. The theory of pH functions is independent of the chemical nature of the ionizing groups: the functions apply equally to molecules with identical ionizing groups (e.g. dicarboxylic acids, as above), to ampholytes (e.g. amino acids), and to molecules or parts of molecules in which the nature of the ionizing groups may not be known (e.g. the active centres of enzymes). For an unsymmetrical dibasic acid there are potentially four ionic forms, four dissociation constants, and thus four pH functions, but these are important in practice only if the pK values of the two dissociating groups are fairly close, as could be the situation at an active centre of an enzyme. If, on the other hand, the pK values are widely separated, as is the case with a typical amino acid, then there is effectively only one intermediate form and a set of three pH functions as above may be considered to apply.

Michel, Hartmut (1948–), German biophysicist; Nobel Laureate in Chemistry (1988) jointly with J. Deisenhofer and R. Huber 'for the determination of the three-dimensional structure of a photosynthetic reaction centre'.

micr+ *see* **micro+** (def. 2).

micra a plural of **micron**.

micRNA *abbr. for* messenger-RNA-interfering complementary RNA (i.e. **antisense RNA**).

micro **1** (concerning something) very small (e.g. micro method). **2** short for a microcomputer.

micro+ **1** *symbol*: μ; the SI prefix denoting 10^{-6} times. **2** *or (sometimes before a vowel)* **micr+** denoting very small or concerned with very small things (e.g. microbiology, microsome); abnormally small, underdeveloped (e.g. microcyte); on a small scale or concerned with small quantities (e.g. microanalysis, microbalance); of a small area or volume, or small part of a larger one (e.g. microenvironment). *Compare* **macro+**. **3** indicating amplification or magnification of something very small (e.g. microphone, microscope). **4** involving the use of a microscope (e.g. micrograph).

microaerophilic **1** describing an aerobic environment with a lower partial pressure of dioxygen than that under normal atmospheric conditions. **2** describing an organism whose maximal rate of growth occurs in such an environment.

microalbuminuria the excretion of plasma albumin in the urine at a rate above the normal range of values (5–20 μg min^{-1}) but below the threshold level (300 μg min^{-1}) for detection by routine dipstick methods and measurable only by radioimmunoassay (or other techniques of comparable sensitivity). The condition is associated with a general increase in vascular permeability and forms a sensitive indicator of diabetic nephropathy.

microanalysis any technique whereby very small amounts of substance may be analysed qualitatively or quantitatively. The term was originally used to indicate analysis of substances in the range 1–10 mg. —**microanalytic** *or* **microanalytical** *adj.*

microassay any technique whereby very small amounts of substance may be assayed. *Compare* **microanalysis**.

microbalance any balance designed to weigh very small quantities, typically between 1 μg and 1 mg.

microbe *a common term for* a microorganism, especially a pathogenic bacterium. —**microbial** *adj.*

microbial collagenase EC 3.4.24.3; *other names*: *Clostridium histolyticum* collagenase; clostridiopeptidase A; collagenase A; collagenase I; an enzyme that catalyses the digestion of native collagen in the triple-helical region at Xaa-|-Gly bonds. Some preference is shown for Gly at P3 and P1′, Pro and Ala at P2 and P2′, and hydroxyproline, Ala, or Arg at P3′ (*see* **peptidase P-sites**). Example (precursor) from *C. perfringens*: database code A36866, 1104 amino acids (125.97 kDa).

microbiological of, pertaining to, or concerned with microbiology; effected by microorganisms.

microbiological assay any assay for a substance, especially an amino acid or vitamin, that is based on the extent of growth of a microorganism for which the analyte in question is an essential growth factor.

microbiology the science concerned with microorganisms, and

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with their interactions with other organisms and the environment. —**microbiologist** *n.*

microbody a cytoplasmic organelle, spherical or oval in shape, and 0.1–1.5 nm across, that is bounded by a single membrane and contains oxidative enzymes, especially those utilizing H_2O_2. Microbodies include **glyoxysomes** and **peroxisomes**.

microbore high-pressure liquid chromatography *or* **microbore HPLC** *a variant of* **high-pressure liquid chromatography** in which a column of only about 1 mm diameter is used. The advantages of the technique include greater sensitivity and a much reduced solvent consumption.

microcalorimeter a **calorimeter** designed to measure continuous power outputs down to 1 μW, or heat pulses down to 200 μJ. —**microcalorimetry** *n.*; **microcalorimetric** *adj.*

microcapsule any very small thin-walled capsule of plastic, wax, etc., containing a liquid, powder, etc., from which the contents may be released (by heat, impact, radiation, dissolution, or other means) in order to fulfil some specific function. *See also* **microencapsulation**.

microcarrier any of a number of preparations of finely particulate, nontoxic, nonrigid, usually transparent material of density close to unity, e.g. dextran-based beads, that enable the growth of animal cells in suspension culture, especially on a large scale. Microcarriers permit the growth of anchorage-dependent cells as a monolayer on the surface of the particles. Generally, the cells may be easily harvested, e.g. by allowing the particles to settle and then treating with a proteinase such as trypsin.

microcell **1** a small, experimentally produced eukaryotic cell-like structure in which a limited amount of genetic material is contained in a micronucleus surrounded by a rim of cytoplasm and an intact cell membrane. It is useful as a vector for the transfer of a small number of chromosomes into a normal cell by virus-induced cell fusion. **2** any small **cell** (def. 2), commonly with a capacity less than 1 mL.

microchemistry chemistry on a very small scale, commonly handling less than 1 mg or 1 mL of material and often requiring special small apparatus. —**microchemical** *adj.*

microcin any of a number of microbial peptide toxins that have antibiotic action. They are of diverse structure and action. Examples include microcin E492, a 6 kDa polypeptide antibiotic. It forms cation-selective channels in planar phospholipid bilayers, leading to a loss of membrane potential. Another example is microcin B17 (precursor): database code MCBA_ECOLI, 69 amino acids (6.01 kDa); residues 1–26 are a propeptide, 27–69 are microcin B17. This is a glycine-rich peptide that inhibits DNA gyrase (*see* **(DNA) topoisomerase** type II).

micrococcal of, pertaining to, or produced by micrococci; being a member of the genus ***Micrococcus***.

Micrococcus a genus of Gram-positive, strictly aerobic, usually nonmotile coccoid bacteria of the family Micrococcaceae. The cells are commonly 1–2 μm in diameter.

microconcentrator a commercial device for the concentration and desalting of 'small' volumes (i.e. ≤2 mL) of biological samples.

microcrystal any very small crystal, especially one that is visible only under a microscope. —**microcrystalline** *adj.*

microcurie *symbol*: μCi *or (formerly)* μc; a unit of (radio)activity or of radioactive material equal to 10^{-6} **curie**.

microdeletion a DNA/chromosomal deletion that is not detectable by conventional techniques such as **Southern blotting** or microscopy.

microdensitometry the measurement of **absorbance** (i.e. optical density) over a very small finite area, such as that viewed by an optical microscope. —**microdensitometric** *adj.*; **microdensitometer** *n.*

microdialyser *or (sometimes, esp. US)* **microdialyzer** a device for **microdialysis**, especially one designed to minimize loss and dilution of samples.

microdialysis dialysis of a sample of small volume (commonly of less than 1 mL).

microdiffusion analysis *see* **Conway microdiffusion method**.

microdissection the dissection of small organisms or parts of organisms by means of mechanically controlled instruments viewed through an optical microscope.

microelectrode any electrode in which the sensitive element is very small and also often needle-like. It is useful for investigation of electrical phenomena in individual cells or in very small volumes.

microencapsulation the act or process of enclosing substances, solutions, etc. in **microcapsules**.

microenvironment a very small domain of the environment, such as that surrounding a single molecule or a functional group of a molecule, a single cell or organism, or a small group of cells or organisms. The term is used especially to distinguish zones of local difference in the overall environment.

microfarad *abbr.*: mfd; *symbol*: μF; a unit of capacitance equal to 10^{-6} **farad**.

microfibre *or (US)* **microfiber** any fibre having a diameter in the range 0.1–1 μm, such as used in making glass microfibre filters.

microfibril any small fibril occurring in biological material that is distinguishable only by electron microscopy, especially one of a set that make up a fibril, e.g. in cellulose. —**microfibrillar** *adj.*

microfibrillar polysaccharide one of three groups of cell-wall polysaccharides characterized by solubility differences: the main component in the plant kingdom is **cellulose** but **chitin** is found in some fungi, β-1,4-mannans in some green algae (e.g. Codiaceae) and β-1,3-xylans in other green algae (e.g. Bryopsidaceae).

microfilament a type of **actin filament** that contributes to the cytoskeleton of eukaryotic cells. Microfilaments are elongated structures consisting of two strands of globular **actin** monomers twisted into a helix with 13.5 molecules per turn. Microfilaments form the major component of the cell's contractile machinery and are implicated in cell division, cell movement, muscle contraction, nerve outgrowth, tubular gland formation, gastrulation, and neurulation. *Compare* **intermediate filament**, **microtubule**.

microfilter **1** any small filter, especially as used in microchemistry. **2** *see* **microporous filter**.

microfiltration filtration with a **microporous filter**.

microflora **1** *a collective name for* very small plants. **2** the flora of a **microhabitat**. **3** *a collective name for* all the microorganisms of a tissue or organ of an animal.

microfluorimeter an instrument for **microfluorimetry**.

microfluorimetry the measurement of intensity of fluorescence over a very small finite area, such as a single cell viewed under an optical microscope. —**microfluorimetric** *adj.*

microforge a device by means of which micropipettes, very small glass tools, etc. can be made while being viewed under a low-power microscope.

microfungus (*pl.* **microfungi**) any fungus whose vegetative thallus or fruiting body is too small to be seen easily with the unaided eye. *Compare* **mould**.

microglobulin **1** any plasma **globulin** molecule or globulin fragment of less than ≈40 kDa, e.g. **Bence-Jones protein**, **β_2-microglobulin**. **2** *a term sometimes used to refer to* 7S immunoglobulins such as IgG. *Compare* **macroglobulin**.

β_2-microglobulin *or* **betamicroglobulin** a human plasma protein, of 11.8 kDa and containing 99 amino-acid residues, that in size, primary structure, and tertiary structure strongly resembles a single domain of the constant region of immunoglobulin molecules: it is a constituent of class I **major histocompatibility complexes**. Plasma levels may be elevated in hepatobiliary disease, chronic active hepatitis, and alcohol-induced liver cirrhosis.

microgram **1** *symbol*: μg *or (esp. in pharmacy)* mcg; a unit of mass equal to 10^{-9} kilogram or 10^{-6} gram; *formerly called* gamma (*symbol*: γ). **2** *an alternative name (sometimes) for* **micrograph**.

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micrograph *or (sometimes)* **microgram** a graphic reproduction of the image of an object as seen through a microscope.

microhabitat any habitat that is small or limited in extent and differs in character from a larger, surrounding habitat.

microheterogeneous describing a preparation of a biopolymer that superficially appears to be homogeneous but that, on refined analysis, shows slight differences in size, sequence, charge, state of aggregation, or other properties of its molecules. Such differences are believed, at least in some instances, to be attributable either to artefactual changes or to genetic differences. —**microheterogeneity** *n.*

microincineration a technique for examining the distribution of minerals in tissue sections or microorganisms. The specimen is placed on a slide, the organic material burned away in a furnace, and the nature and position of the mineral ash determined by microscopy.

microinject to inject liquid into a single cell or nerve fibre using a micropipette. —**microinjection** *n.*

microiontophoresis **iontophoresis** (def. 2) applied to very small areas of tissue.

micro-Kjeldahl method an adaptation of the **Kjeldahl method** for determining small amounts of nitrogen, in the range 0.1–1.0 mg. A correspondingly small flask, commonly known as a **micro-Kjeldahl flask**, is used for the digestion, and a **Markham still** may be used for the steam distillation.

microlitre *or (esp. US)* **microliter** *symbol*: μL *or* μl; a unit of volume equal to 10^{-6} litre; *formerly called* **lambda** (*symbol*: λ).

micromanipulation the techniques and practice of performing very delicate operations, such as microdissection, microinjection, or the isolation of single cells, under an optical microscope, usually with the aid of a **micromanipulator**.

micromanipulator an instrument used in conjunction with an optical microscope for holding and manipulating very small instruments and specimens in the field of view.

micrometer **1** any instrument or device for measuring very small distances or angles. **2** *or* **micrometer gauge** a device for measuring small distances, thicknesses, diameters, etc. with great accuracy. **3** *the US spelling of* **micrometre**.

micrometer burette a **micrometer syringe** adapted for use as a burette.

micrometer pipette a **micrometer syringe** adapted for use as a pipette.

micrometer screw a screw with a fine thread of accurate and consistent pitch.

micrometer syringe a syringe for the accurate delivery of small volumes of liquid in which the plunger of the syringe is driven by a calibrated micrometer screw.

micrometre *or (US)* **micrometer** *symbol*: μm; a unit of length equal to 10^{-6} metre; *formerly called* **micron** (*symbol*: μ).

micromicro+ *symbol*: μμ; *a former name for* **pico+**.

micromodification alteration of the covalent structure of a macromolecule, especially a histone, by the addition of various groups, e.g. acetyl, methyl, phosphate, after the initial biosynthetic process is terminated.

micromolar *symbol*: μM *or* μM; describing a solution containing one micromole of solute per litre of solution, or a specified multiple or fraction thereof; used also of an amount-of-substance concentration similarly expressed.

micromole *symbol*: μmol; a unit of amount of substance equal to 10^{-6} mole.

micromolecule any (type of) molecule composed of a relatively small number of atoms. In practice the term is usually taken to mean any (type of) molecule that is capable of passing through the pores of dialysis tubing (as generally used) and that thus has a mass less than about 10 kDa. —**micromolecular** *adj.*

micron (*pl.* **microns** *or* **micra**) *symbol*: μ; *a former term for* **micrometre**.

micronucleus a eukaryotic cell nucleus with less than the normal complement of chromosomes, produced experimentally by incubation of a cell with colchicine. —**micronuclear** *adj.*

micronutrient any chemical element that is required by living organisms in tiny quantities only, also known as **trace element**. The term is often extended to include organic compounds such as vitamins.

microorganism any noncellular or unicellular (including colonial) organism, most of which are too small to be seen with the unaided eye. Microorganisms comprise bacteria (including cyanobacteria), lichens, microfungi, protozoa, rickettsiae, virinos, viroids, and viruses, and also some algae; all prokaryotes are included. *See also* **microbe**.

microperoxisome *(sometimes)* a type of small **peroxisome**, 150–250 nm in diameter, found in all mammalian cells.

micropinocytosis *(sometimes)* a form of **pinocytosis** occurring in higher animals, especially in the transfer of dissolved macromolecules from the blood to the cytoplasm of cells, in which the pinosomes formed are very small (**micropinosomes**) and can only be observed in the electron microscope.

micropipette *or (US)* **micropipet** any pipette calibrated to contain or deliver a volume in the range 5–500 μL.

micropore any pore (in a gel or porous solid) whose width does not exceed about 2.0 nm. *Compare* **macropore**, **mesopore**. —**microporous** *adj.*

microprocessor a single integrated electronic circuit designed to carry out a specific set of operations, e.g. as the central processor of a computer or a control system.

microsatellite a repeating DNA segment that is similar to a **minisatellite** except that the overall range of size is smaller and the base core repeat unit involves a two or four nucleotide pair repeat motif. They are so named because of their resemblance to **satellite DNA** in having tandem repeats. The number of copies of the repeats varies not only between individuals but also between the two chromosomes of a pair.

microscope an instrument consisting of a lens or a combination of lenses that uses light or other electromagnetic radiation to make enlarged images of objects that are invisible to, or not easily seen by, the unaided eye. *See also* **electron microscope**, **phase-contrast microscopy**.

microscopic **1** of a size that is not visible (in detail) to the unaided eye. **2** concerned with small units. **3** relating to the behaviour of individual molecular entities. **4** *or* **microscopical** of, pertaining to, or using a microscope. *Compare* **macroscopic**. —**microscopically** *adv.*

microscopic equilibrium constant any constant describing the equilibrium of the interconversion of two particular molecular entities. *Compare* **intrinsic constant**, **macroscopic equilibrium constant**.

microscopic reversibility a thermodynamic principle requiring that at equilibrium the reaction pathway for the reverse of any particular chemical reaction is the exact opposite of the pathway for the forward reaction, i.e. both forward and backward reactions must pass through the same transition states or intermediates and occur with equal frequency.

microscopy the art and practice of using a microscope; investigation with a microscope.

microsecond *symbol*: μs; a unit of time equal to 10^{-6} second.

microsequenator an apparatus for microsequencing (*see* **microsequence**).

microsequence to **sequence** (def. 3) a biopolymer using a very small sample, e.g. 5–100 pmol of a protein.

microsolute *an operational term used to describe* any diffusible solute in a solution that also contains nondiffusible macromolecular solute(s).

microsomal of, pertaining to, or containing **microsomes**; being in the **microsomal fraction** of a homogenate of a cell or tissue.

microsomal fraction *an operational term for* the subcellular fraction of a homogenate of a eukaryotic cell or tissue that, on differential centrifugation, is sedimented at 10^5 *g*; the fraction from some tissues, such as liver, although consisting largely of microsomes, commonly also contains free ribosomes and fragments of the plasma membrane, of the Golgi apparatus, of mitochondria, and of other subcellular structures. The morpho-

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logical constituents differ according to the tissue from which the fraction was derived.

microsome any of the small, heterogeneous, artefactual, vesicular particles, 50–150 nm in diameter, that are formed when some eukaryotic cells are homogenized and that sediment on centrifugation at 10^5 *g*. Microsomes are formed mostly from disrupted endoplasmic reticulum membranes but some arise from the plasma membrane. Those formed from rough endoplasmic reticulum are studded with ribosomes on the outside (**rough microsomes**); those formed from smooth endoplasmic reticulum and from plasma membrane have no adhering ribosomes (**smooth microsomes**).

microspectrophotometer an instrument, consisting of a microscope and a spectrophotometer, used for measuring light of selected frequencies passing through, or reflected from, a very small specimen, e.g. a cell or a subcellular structure.

microspectrophotometry **spectrophotometry** applied to a very small specimen, using a microspectrophotometer. —**microspectrophotometric** *adj.*

microsphere one of a preparation of spherical particles of known and uniform size, usually in the range 10–40 μm in diameter, and prepared from, e.g., serum albumin or an ion-exchange resin, that may be labelled with an appropriate radionuclide and used in studies of the circulation of the blood in health or disease.

microspore the smaller of the two types of spores produced by the heterosporous plants. In seed plants the microspore is the cell from which the pollen grain develops. —**microsporous** *adj.*

microstructure *an alternative term for* **fine structure**.

microsyringe a syringe for delivering volumes of gases or liquids in the range 0.1–500 μL.

microtome an instrument for cutting thin sections of objects, e.g. tissues or cells, preparatory to microscopic observation.

microtrabecular lattice an irregular, three-dimensional lattice of very fine strands, up to 15 nm in diameter, sometimes termed **microtrabeculae**, that can be visualized in the cytoplasmic ground substance of eukaryotic cells by high-voltage electron microscopy. It forms part of the cytoskeleton.

microtubule any of the long, generally straight, hollow tubes of internal diameter 12–15 nm and external diameter 24 nm found in a wide variety of eukaryotic cells. Each consists (usually) of 13 protofilaments of polymeric **tubulin**, staggered in such a manner that the tubulin monomers are arranged in a characteristic helical pattern on the microtubular surface, and with the α/β axes of the tubulin subunits parallel to the long axis of the tubule. Microtubules exist in equilibrium with a pool of tubulin monomers in the cytoplasm and can be rapidly assembled and disassembled in response to various physiological stimuli; there are also a number of **microtubule-associated proteins**. The majority of microtubules in a cell appear to be initiated at **microtubule-organizing centres** and some may also become attached to the **kinetochores**. Microtubules are concerned in force generation in cilia and flagella, where they exist in a characteristic 9 + 2 array (a ring of nine doublet microtubules with two single microtubules in the centre), and the integrity of the microtubule network appears to be necessary for certain aspects of mitotic spindle function and for the saltatory movement of cell organelles. *Compare* **intermediate filament, microfilament**.

microtubule-associated protein *abbr.*: MAP; any protein that binds to **microtubules** and modifies their properties, including proteins that induce polymerization of purified tubulin and become associated with the newly formed microtubules. Many different kinds have been found, including structural proteins and motor proteins. MAP 1 is a structural protein involved in the filamentous cross-bridging between microtubules and other skeletal elements. Example, MAP 1A from rat: database code MAPA_RAT, 2774 amino acids (299.20 kDa). The role of MAP2 is unclear; in neuronal cells it is confined to the cell body and dendrites. It changes structurally during development by alternative splicing mechanisms. Example from rat: database code MAP2_RAT, 1830 amino acids (198.83 kDa). **Dynein** is an example of a motor protein MAP. *Compare* **tau protein**. *See also* **MAP kinase**.

microtubule-organizing centre a region near the centre of a eukaryotic cell consisting typically of two **centrioles** at right angles to each other and surrounded by a complex of associated proteins. The centrioles and their satellite proteins serve as initiating sites for the assembly of microtubules.

microvillin a protein of the microvilli of rat mammary cells of M_r 200 000.

microvillus (*pl.* **microvilli**) any of the very small, finger-like projections that occur on the exposed surfaces of epithelial cells, especially where cellular function requires a maximal surface area for absorption or secretion, as in the proximal renal tubule and the small intestine, where they constitute the brush border. The projections are about 1–2 μm long and 100 nm in diameter. The core of a microvillus contains a bundle of about 40 actin filaments of uniform polarity with their 'barbed' (+) ends anchored in a cap of ill-defined amorphous material in the microvillar tip. At the base the actin filaments extend into the perpendicular network, also made up largely of actin, known as the terminal web. In the core the actin filaments are bound together by the actin-binding proteins fimbrin and villin. The renal and intestinal microvilli contain a wide range of hydrolases that are integral membrane proteins; their hydrophilic domains, containing the catalytic sites, face outwards from the cell. —**microvillar** *adj.*

microvolume a very small volume, commonly in the range 1–100 μL.

microwave radiation electromagnetic radiation of wavelengths in the range 1–300 mm (frequencies 1–300 GHz), lying between infrared radiation and most radiofrequency radiation.

middle molecule *a term sometimes used for* any compound in the range 350–2000 Da that accumulates in the body fluids of persons with uremia.

middle T antigen *see* **T antigen** (def. 1).

midkine *other names*: neurite outgrowth-promoting protein, midgestation and kidney protein, amphiregulin-associated protein (*abbr.*: ARAP); a heparin-binding growth/differentiation factor with neurite-promoting activity. It is a cell-surface or basement-membrane protein, induced by retinoic acid and similar to **pleiotrophin**. The midkine gene product is primarily detected in the embryonic period, whereas pleiotrophin is expressed most strongly in the early neonatal period. Example from human (precursor): database code MKHUMAN, 143 amino acids (15.58 kDa); residues 1–20 are the signal, 21–143 midkine.

midpoint **1** the point on a line, or a graph, that is equidistant from either end of the line or from two inflections in the graph. **2** a point in time that is half way between the beginning and the end of an event, or a series of events.

midpoint potential the **electrode potential**, at a given pH and temperature and 1 atm H_2, at the midpoint of a redox titration when the activities of the reductant and the oxidant are equal.

MIF *abbr. for* **1** (macrophage) migration inhibition factor. **2** melanotropin release-inhibiting factor (i.e. **melanostatin**).

mifepristone *see* **RU-486**.

migratase *an old name for* **mutase**; e.g. lysolecithin migratase is an old name for lysolecithin acylmutase (EC 5.4.1.1).

migrate *(in chemistry)* (of atoms, ions, or molecules) to move from one region of a solution to another, or from a solution in one compartment to a solution in another compartment, under the influence of an electric or a centrifugal field or by diffusion. —**migration** *n.*

migration inhibition factor *abbr.*: MIF; *see* **(macrophage) migration inhibition factor**.

MIH *abbr. for* melanotropin release-inhibiting hormone (i.e. **melanostatin**).

MIL the avian homologue of ***RAF***; v-*mil* is the oncogene of the avian retrovirus Mill-Hill-2, which also carries v-*myc*. It codes for a serine/threonine kinase of the *RAF/MOS* subfamily of

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unknown function but exhibiting homology with Src and related proteins (*see* **src**). Example, database code KMIL_CHICK, 647 amino acids (73.12 kDa).

milieu (*pl.* **milieus** *or* **milieux**) environment or setting.

milieu intérieur *(French)* the internal environment of a multicellular organism that surrounds the tissues and cells.

milk **1** the white liquid produced and secreted by the mammary glands of mature female mammals for the nourishment of their young. The milk of certain mammals, especially cows, is used as a food by humans, either as liquid milk or in the production of butter, cheese, etc. **2** any of various natural or manufactured liquids that have the appearance or consistency of milk, e.g. coconut milk, milk of magnesia. **3** to squeeze or draw milk from; to yield milk. —**milky** *adj.*

milk factor *an alternative name for* **Bittner factor**.

milk sugar *an old name for* D-**lactose**.

Miller index *(in crystallography)* any of a set of three integers that determine the position of a face, or internal plane, of a crystal in relation to three crystallographic axes. They are determined on the basis of the reciprocals of the intercepts of the face or plane on the crystallographic axes. [After W. H. Miller (1801–80).]

milli+ **1** *symbol*: m; an SI prefix denoting 10^{-3} times. **2** *prefix* denoting one-thousandth.

millicurie *symbol*: mCi *or (formerly)* mc; a unit of (radio)activity or of radioactive material equal to 10^{-3} **curie**.

milliequivalent *symbol*: mequiv *or* meq *or* mEq; a unit of amount of substance equal to 10^{-3} **equivalent** (def. 3); (mmol recommended).

milligram *symbol*: mg; a unit of mass equal to 10^{-6} **kilogram** or 10^{-3} gram.

millilitre *or (US)* **milliliter** *symbol*: ml *or* mL; a unit of volume equal to 10^{-3} **litre**. It is now identical to the cubic centimetre; i.e. 1 mL = 1 cm^3 = 10^{-6} m^3.

millimetre *or (US)* **millimeter** *symbol*: mm; a unit of length equal to 10^{-3} **metre**.

millimetre of mercury *symbol*: mmHg; a non-SI unit of pressure defined as the pressure exerted by a column exactly 1 mm high of a fluid of density that is exactly 13.5951 g cm^{-3} in a place where the acceleration of free fall is exactly 980.665 cm s^{-2}. Its use is deprecated. 1 mmHg = 1 torr = 133.32 pascal.

millimicro+ *a former name for* **nano+**.

millimicron (*pl.* **millimicrons** *or* **millimicra**) *symbol*: mμ; *a former name for* **nanometre**.

millimolar *symbol*: mM *or* mM; describing a solution containing one millimole per litre of solution, or a specified multiple or fraction thereof; the term is also used of an amount-of-substance concentration similarly expressed.

millimole *symbol*: mmol; a unit of amount of substance equal to 10^{-3} **mole**.

Millipore **1** *the proprietary name for* a range of microporous and other types of membrane filters manufactured by the Millipore Corporation. **2** a water purification system, manufactured by the same company and based on reverse osmosis.

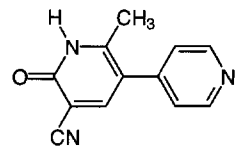
millisecond *symbol*: ms; a unit of time equal to 10^{-3} **second**.

Millon's reaction the formation of red complexes when compounds containing the hydroxybenzene group are heated with **Millon's reagent**. The reaction is given by proteins that contain one or more tyrosine residues. [After Auguste Millon (1812–67), French chemist.]

Millon's reagent a 15% solution of mercuric sulfate in 15% sulfuric acid. This is added to the test sample solution, which is then heated in a boiling water bath for 10 min. After cooling, a 1% aqueous solution of sodium nitrite is added to the cooled reaction mixture. Originally it was a solution of mercuric nitrate in 50% nitric acid containing some nitrous acid. It gives **Millon's reaction** with compounds containing the hydroxybenzene group.

Mills perspective representation *or* **Mills representation** a diagrammatic way of unambiguously representing the structural formulae of carbohydrates and their polycyclic derivatives to show on a plane surface the relative configurational arrangements of substituents and bridges. It is particularly useful in instances where the **Haworth representation** is inconvenient, e.g. for depicting saccharides with substituents that bridge two positions on the ring. The carbohydrate in question, or its derivative, is drawn with single rings and fused rings in the plane of the surface, and with bonds to substituents or bridges above or below the plane of the rings drawn with dark lines (often wedge-shaped) or broken lines, respectively (as is customary in representations of steroids and terpenes). Hydrogen atoms in the angular positions at ring junctions are always shown but those at points of substitution may be omitted. Like **Fischer projections**, but unlike Haworth representations, Mills representations may be rotated in the plane of the paper without alteration of their significance. It was proposed primarily for carbohydrate structures, but resembles systems used for other types of molecule, e.g. steroids.

milrinone 1,2-dihydro-6-methyl-2-oxo-5-(4-pyridinyl)nicotinonitrile; a phosphodiesterase inhibitor with vasodilating and cardiostimulant activity.



Milstein, César (1927–), Argentinian-born British biochemist and immunologist; Nobel Laureate in Physiology or Medicine (1984) jointly with N. K. Jerne and G. J. F. Köhler 'for theories concerning the specificity in development and control of the immune system and the discovery of the principle for production of monoclonal antibodies'.

mimetic imitating closely.

+mimetic *suffix (esp. in pharmacology)* denoting having a similar effect to the substance or action indicated.

min *symbol for* minute.

mince **1** to disrupt tissue with a **tissue grinder** to the level at which there is extensive, but incomplete, rupture of cells. **2** the preparation resulting from the action of a coarse tissue grinder.

mineral **1** any naturally occurring inorganic substance of a type often obtained by mining, e.g. coal, stone, petroleum. **2** any of a class of naturally occurring inorganic substances, of definite chemical composition and physical properties and often crystalline in character. **3** of, pertaining to, or being a **mineral** (def. 1, 2).

mineralize *or* **mineralise** (of an organic material) to convert into, or impregnate with, a mineral or minerals. —**mineralization** *or* **mineralisation** *n.*

mineralocorticoid *or* **mineralocorticosteroid** any naturally occurring or synthetic hormonal **corticosteroid** that acts primarily on water and electrolyte balance by promoting the renal retention of sodium ions and excretion of potassium ions. Mineralocorticoids are produced in the outer layer (zona glomerulosa) of the adrenal cortex. **Aldosterone** is the most potent of the naturally occurring mineralocorticoids. *Compare* **glucocorticoid**.

mini+ *comb. form* denoting miniature; of smaller than usual dimensions.

minicell **1** a small cell-like body arising from a polar region of a rod-shaped bacterium by aberrant cell division. It is spherical or near-spherical in shape and devoid of chromosomal DNA; hence it does not grow or divide and is normally unable to synthesize nucleic acid or protein (but may do so if a plasmid is introduced). **2** an experimentally produced eukaryotic cell in which an intact cell nucleus is surrounded by scant cytoplasm and a cell membrane. It is prepared by enucleation of a normal mononucleate cell.

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miniexon a small exon, as found in the troponin T gene.

minigastrin a form of the peptide hormone **gastrin** that contains 14 amino-acid residues. It has been isolated from tumour tissue and correspoinds to residues 5–17 of human gastrin 1, having the sequence LEEEEEAYGWLDFH-amide.

minima a plural of **minimum**.

minimal of, being, or constituting the minimum; the least possible.

minimal medium a (synthetic) culture medium containing only those compounds essential for the growth of a wild-type organism and that is not able to support growth of an auxotroph.

minimum (*pl.* **minimums** *or* **minima**) **1** the least quantity, degree, or value possible or permissible. **2** *(in mathematics)* a value of a function that is less than that of any neighbouring value. **3** of, or pertaining to, a minimum or minimums.

minimum inhibitory concentration *abbr.*: MIC; the lowest concentration of a drug, or other substance, that just inhibits the growth of a given test organism (bacterium, etc.) in defined conditions.

minimum lethal dose *abbr.*: MLD; the minimum dose of a toxic substance, or organism, that will kill, within a specified time, all the animals in a test group to which it is administered.

minimum (relative) molecular mass *or (formerly)* **minimum molecular weight** the (relative) molecular mass of a compound as determined by the assay of one of its structural elements, e.g. a metal atom, a ligand, a terminal residue, etc., assuming that there must be at least one such structural element in each molecule of the compound.

minisatellite a repeat DNA segment comprising short head-to-tail tandem repeats giving **variable number tandem repeat**-type polymorphisms, with approximate size between 1 and 30 kb. The name derives from the fact that repeat DNA segments were originally found in **satellite DNA**, but the overall size of the minisatellite segments and the length of individual repeats are smaller, and satellite peaks are not seen on centrifugation.

minivial a very small vial, especially a low-capacity container that can be inserted into a normal-sized sample vial used in liquid scintillation counting, to enable the (radio)activity of small-volume samples to be determined more efficiently.

minor base *see* **minor nucleoside**.

minor groove the smaller and shallower of the two grooves on the surface of a double-helical DNA molecule. *Compare* **major groove**.

minor nucleoside a nucleoside containing any of a group of purine or pyrimidine bases that occur in small amounts in most nucleic acids but in relatively large amounts in transfer RNA molecules; they are sometimes known as '**odd bases**'. These are a characteristic feature of **transfer RNA** from all organisms. The modifications range from the simple methylation of bases or ribose sugar residues to very complex substitutions. All modifications take place after transcription of the transfer RNA genes. The importance of the modifications is thought to be related to the stability of the tertiary structure. A typical modified nucleoside is **pseudouridine**. *See also* **wyosine**.

minuend *(in mathematics)* the number (or quantity) from which another number (or quantity), the subtrahend, is to be subtracted.

minus end the end of a microtubule or actin filament at which the addition of monomers occurs least readily; the 'slow-growing' end of a microtubule or actin filament. The minus end of an actin filament is also known as the pointed end. *Compare* **plus end**.

minus 10 region and **minus 35 region** regions in the **promoter** defined by the number of nucleotides 5′ from the first nucleotide transcribed, i.e. on the **coding strand**. The first nucleotide (the start site) of a transcribed DNA sequence is denoted as +1, the second +2; the nucleotide preceding the start site is denoted as –1. The most conserved sequence upstream (towards the 5′ terminus) of DNA in *Escherichia coli* is a hexamer centred at the –10 position (*see* **Pribnow box**). It has a consensus sequence of TATAAT in which the leading TA and final T are highly conserved. –35 is the centre point of a consensus sequence involved in RNA polymerase recognition, TTGACA.

minus strand **1** the complementary strand to the parental polynucleotide strand – the **plus strand** (def. 1) – in bacteriophages whose genomes consist of duplex RNA. **2** any polynucleotide strand (RNA or DNA) in a viral genome that is complementary to the virus-specified mRNA – the **plus strand** (def. 2). **3** *(sometimes) an alternative term for* **coding strand** (of genetic duplex DNA).

minute **1** *symbol*: min; a non-SI unit of time equal to 60 seconds. **2** *symbol*: ′; a unit of plane angle equal to (π/10 800) radians, or 0.291 milliradians. There are 60 seconds (of arc) in one minute (of arc), and 60 minutes in one degree (of arc). **3** *(in genetics)* an empirical unit of distance between genes in a bacterial chromosome, being a measure of the time taken, in minutes, for the transfer of a particular gene during bacterial conjugation relative to an arbitrarily standardized selected origin.

7-minute phosphate *or* **10-minute phosphate** *see* **labile phosphate**.

MIP *abbr. for* macrophage inflammatory protein.

misacylate *or* **mischarge** to acylate (a transfer RNA molecule) with an aminoacyl group other than the specific one. —**misacylation** *n.*

mischarge *an alternative term for* **misacylate**.

miscible (of two or more particular liquids) capable of being mixed together to give a homogeneous liquid. Particular liquids may be completely miscible or miscible only in certain proportions. *See also* **proofreading**. —**miscibility** *n.*

mismatch repair a system for the correction of errors introduced during DNA replication when an incorrect base, which cannot form hydrogen bonds with the corresponding base in the parent strand, is incorporated into the daughter strand. **Excinucleases** recognize a pair of non-hydrogen-bonded bases and cause a segment of polynucleotide chain to be excised from the (less methylated) daughter strand, thereby removing the mismatched base. The resulting gap is then filled by the actions of DNA polymerase I and DNA ligase.

mispairing the occurrence of a base in one polynucleotide strand of duplex DNA that is not complementary to the corresponding base in the second polynucleotide strand.

missense codon a particular codon that has been altered so that it codes for an amino-acid residue different from the one for which it normally codes.

missense mutation any mutation causing a base substitution in a gene that results, following transcription and translation, in the incorporation of an incorrect amino-acid residue at a specific point in the polypeptide gene product. *Compare* **nonsense mutation**, **samesense mutation**.

mistranslation the insertion at a specific point in a polypeptide chain of an amino-acid residue that is not indicated by the corresponding codon in the mRNA molecule that is being translated.

MIT *abbr. for* (3-)monoiodotyrosine.

Mitchell, Peter Dennis (1920–92), British biochemist; Nobel Laureate in Chemistry (1978) 'for his contribution to the understanding of biological energy transfer through the formulation of the chemiosmotic theory'.

Mitchell hypothesis the hypothesis that mitochondrial systems can be driven by proton and electrical gradients that build up across membranes, a mechanism now referred to as **chemiosmotic coupling**.

mitochondria the plural of **mitochondrion**.

mitochondriac a biochemist with a chronic and unusually intense interest in mitochondria.

mitochondrial carrier protein any of various proteins involved in the translocation of small molecules across the mitochondrial inner membrane. Many are translocases using an

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antiport mechanism, and include carriers for pyruvate (antiport molecule is OH^-), phosphate (malate), citrate (malate), phosphate (OH^-), ADP (ATP), aspartate (glutamate), and malate (2-oxoglutarate); an example is ADP/ATP translocase 1 of yeast: database code ADT1_YEAST, 309 amino acids (34.08 kDa); this is an integral inner membrane protein, comprising a homodimer with three homologous domains in each subunit. *See also* **OGCP**.

mitochondrial DNA *abbr.*: mtDNA; DNA that is contained, replicated, and expressed in mitochondria. Mitochondrial DNA is double-stranded in almost all organisms studied; that from mammals has a contour length of ≈5 μm, about 15 kilobases, while that from protozoa and fungi is about five times larger. In yeast, mitochondrial DNA codes for two types of rRNA molecules, about 26 types of tRNA molecules, and about 10 proteins (which represent only about 5% of the total mitochondrial protein). The code in mitochondrial DNA differs in some respects from that in nuclear DNA (*see* **genetic code**).

mitochondrial fraction *an operational term* for the more rapidly sedimenting components (for example 10 000–15 000 *g* for 30 min) of the **cytoplasmic fraction** of a homogenate of eukaryotic cells or tissue. It generally consists predominantly of mitochondria but may also contain varying numbers of secretion granules, lysosomes, microbodies, or other intracellular organelles.

mitochondrial plasmid DNA a distinct class of genetic elements, found in certain wild-type strains of *Neurospora*, that show virtually no sequence homology with standard mitochondrial DNA (mtDNA) in DNA–DNA hybridization experiments and achieve high copy number without suppressive behaviour towards wild-type mtDNA.

mitochondrial matrix the gel-like material, with considerable fine structure, that lies in the matrix space, or lumen, of a **mitochondrion**. It contains the enzymes concerned with fatty-acid oxidation and enzymes of the tricarboxylic-acid cycle.

mitochondrial processing peptidase EC 3.4.99.41; an enzyme that catalyses the cleavage of the leader peptide from precursor proteins imported into the mitochondrion, typically ones with Arg in position P2 (*see* **peptidase P-sites**). These enzymes resemble in sequence **premurein-leader peptidase**. Example from *Neurospora crassa*; catalytic subunit (precursor): database code MPP1_NEUCR, 577 amino acids (62.96 kDa); enhancer subunit (precursor): database code MPP2_NEUCR, 476 amino acids (52.50 kDa). Both are transmembrane proteins; the enzyme requires the presence of divalent cations for activity.

mitochondrial RNA *abbr.*: mtRNA; any RNA molecules that are complementary to mitochondrial DNA.

mitochondrial state *see* **respiratory state (of mitochondria)**.

mitochondrion (*pl.* **mitochondria**) a semiautonomous, self-replicating organelle that occurs in varying numbers, shapes, and sizes in the cytoplasm of virtually all eukaryotic cells. It is notably the site of tissue respiration (*see* **respiratory chain**, **oxidative phosphorylation**). Conventionally, mitochondria are represented as elongated cylinders with a diameter of 0.5–1.0 μm; however, in living cells they show great mobility and plasticity, in some cells forming long, moving chains while in other types of cells being fixed in position near sites of high ATP consumption; e.g. in cardiac muscle they are packed between the myofibrils while in a sperm they are tightly wrapped around the flagellum. Mammalian hepatocytes each contain 1000–2000 mitochondria, which occupy roughly 20% of the cell volume. A mitochondrion has two functionally distinct lipid-bilayer membrane systems, the outer one completely surrounding the whole organelle and the inner one being infolded into **cristae**. These membrane systems define two mitochondrial compartments: the mitochondrial matrix and the intermembrane space. The matrix contains enzymes for the oxidation of pyruvate and fatty acids and for the tricarboxylic-acid cycle; it also contains the mitochondrial DNA and the enzymes and structures necessary for expression of the mitochondrial genes. The inner mitochondrial membrane contains the enzymes of the respiratory chain, ATP synthetase, and specific transport proteins. The intermembrane space contains a number of kinases. The outer membrane, which is permeable to molecules of up to 10 kDa, contains monoamine oxidase, cytochrome b_5, a number of transferases, and a fatty-acid elongation system. The mitochondrion was formerly known as a **chondriosome** and by numerous other names. *See also* **cercidosome**. —**mitochondrial** *adj.*

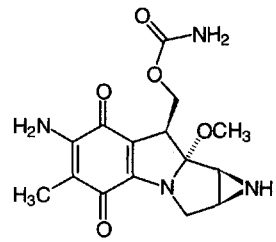
mitochrome a chromoprotein, or mixture of chromoproteins, released from mitochondria *in vitro* after ageing or other degradative processes. They are hemoproteins of ≈105 kDa with 1 atom of Fe per molecule, and are thought to inhibit *in vitro* oxidative phosphorylation.

mitogen any substance or agent that induces or stimulates **mitosis**. —**mitogenic** *or* **mitogenetic** *adj.*

mitogenic protein *abbr.*: MP; *an alternative name for* **interleukin 1**.

mitogillin EC 3.1.27.–; *other names*: allergen I/A; IgE-binding ribotoxin; a purine-specific ribonuclease that attacks 28S rRNA. The protein is a powerful allergen, an inhibitor of eukaryotic protein synthesis, and has anti-tumour activity. Its action is similar to **restrictocin** and ribonuclease U2. Example (precursor) from *Aspergillus restrictus* and *A. fumigatus*: database code RNMG_ASPRE, 176 amino acids (19.57 kDa).

mitomycin C a 334 Da antibiotic and the principal member of a group of closely related aziridine antibiotics (mitomycins) produced by *Streptomyces caespitosus*. Mitomycin C is toxic to bacteria and mammalian cells and possesses antineoplastic activity. When administered, mitomycin C undergoes intramolecular rearrangement and reduction within cells to form a bifunctional alkylating agent that irreversibly cross-links the two strands of duplex DNA molecules, thereby inhibiting DNA synthesis.



mitoplast a structure consisting of the inner membrane and the matrix of a **mitochondrion**. It is formed by removing the outer membrane and the intermembrane material by treatment of a mitochondrion with nonionic detergents under defined conditions.

mitoribosome any of the bacterial-like **ribosomes** found in mitochondria.

mitosis *or* **karyokinesis** the division of a eukaryotic cell nucleus to produce two daughter nuclei that contain identical numbers of chromosomes and that are identical genetically to the parent nucleus except where crossing over or mutation has occurred. It is divided into five main stages: **prophase**, **prometaphase**, **metaphase**, **anaphase**, and **telophase**. Mitosis is normally accompanied by **cytokinesis** leading to division of the cell. *Compare* **meiosis**. —**mitotic** *adj.*

mitotic coefficient *or* **mitotic index** the proportion of cells in a population that are in **mitosis** at a given time.

mitotic recombination *or* **somatic crossing over** crossing over between homologous chromosomes during mitotic division of a diploid somatic cell. The result of such a recombination will be imperceptible if the cell is homozygous at the loci exchanged but may produce a marked effect if the dividing cell is

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heterozygous at these loci. *See also* **Holliday junction recombination**.

mitotic spindle *see* **spindle**.

mixed acid fermentation a particular mode of bacterial fermentation of glucose that is characteristic of many members of the Enterobacteriaceae, e.g. *Escherichia*, *Salmonella*, and *Shigella*. It yields, as principal products, acetic, formic, lactic, and succinic acids, in varying proportions according to the organism and growth conditions.

mixed anhydride any **acid anhydride** formed between two different acids.

mixed-bed deionizer an apparatus for removing electrolytes from impure water (or an aqueous solution) and containing an intimate mixture of anion- and cation-exchange resins. It is frequently fitted with a device for measuring the electrolytic conductivity of the effluent.

mixed-bed resin *a common but imprecise term for* an intimate mixture of anion- and cation-exchange resins as used in a mixed-bed deionizer.

mixed-function oxidase *or* **mixed-function oxygenase** *an older term for* **monooxygenase**.

mixed indicator **1** a mixture, in definite proportions, of two acid–base indicators, or of an indicator and a dye, chosen so as to produce a sharp colour change over a narrow range of pH values. **2** a mixture, in definite proportions, of two or more acid–base indicators chosen so as to produce a series of colour changes over an extended range of pH values.

mixed inhibition *or* **mixed-type inhibition** inhibition of the activity of an enzyme that yields complex kinetic data that cannot be clearly categorized as either competitive or non-competitive. This can result e.g. when the enzyme–substrate–inhibitor complex undergoes the catalytic process slowly, or where binding of the inhibitor changes both k_{cat} and K_m.

mixed inhibitor *or* **mixed-type inhibitor** any inhibitor that produces **mixed inhibition** of the activity of an enzyme.

mixed labelled describing a specifically isotopically labelled compound that has more than one type of modified atom, e.g. $[^{13}C]H_3–CH_2[^{18}O]H$.

mixed-lymphocyte reaction *or* **mixed-leukocyte reaction** the reaction that occurs when leukocytes from two genetically differing individuals are cultured together. Small lymphocytes are transformed into immature blast cells, with synthesis of DNA, to an extent that is related to the degree of disparity between the histocompatibility antigens of the cell donors. This reaction forms the basis of a test for the acceptability of an allograft.

mixed triacylglycerol *or (formerly)* **mixed triglyceride** any **triacylglycerol** in which individual molecules contain acyl residues of more than one kind.

mixed-type inhibition *an alternative term for* **mixed inhibition**.

mixed-type inhibitor *an alternative term for* **mixed inhibitor**.

mixotropic series a series of solvents arranged on the basis of their ability to form hydrogen bonds. It is based on the extent to which two given solvents in this series will mix; near neighbours in the series are **isopartitive**.

mixture *(in chemistry)* homogeneous or heterogeneous material in any physical state that consists of two or more chemical components that have no firm chemical bonding between them and that are physically separable.

MK *abbr. for* menaquinone.

mks system *or* **MKS system** *abbr. for* metre–kilogram–second system (of electrical units).

mL *or* **ml** *symbol for* millilitre.

MLD *abbr. for* minimum lethal dose.

M line *see* **sarcomere**.

mM *or* mM *symbol for* millimolar.

M macroglobulin a paraprotein of IgM type that is produced by individuals with Waldenström's macroglobulinemia.

mmHg *symbol for* the conventional **millimetre of mercury**.

mmol *symbol for* millimole.

MMP *abbr. for* matrix metalloproteinase.

MMPI *abbr. for* matrix metalloproteinase inhibitor.

MMTV *abbr. for* mouse mammary tumour virus.

Mn *symbol for* manganese.

mnemonic enzyme mechanism *or* **mnemonical enzyme mechanism** an enzyme mechanism proposed to explain cooperativity towards substrate shown by monomeric enzymes with only one substrate-binding site. In this mechanism free enzyme is considered to exist in two conformations, I and II, that are only relatively slowly interconvertible and that differ in their substrate-binding affinities; the binding of substrate induces a change of the enzyme to a third conformation, III, which reverts to conformation I when product is released. The behaviour of the system depends on the rate of interconversion of I and II and on the relative rates at which these forms can bind substrate. If the binding by I is more rapid than that by II, the system will show positive cooperativity, i.e. the enzyme has 'remembered' the catalytically more effective conformation; if the converse, the system will show negative cooperativity.

MNSs system one of the blood-group systems of humans, in which the antigens are the **glycophorins** of the erythrocytes. The MN system was the second human-blood-group system to be discovered, the first being the ABH system (*see* **ABH antigens**). The M and N antigenic sites are poorly immunogenic and antibodies to M and N antigens do not normally occur in the blood. The determinants are located at the N terminus of glycophorins A and B (GPA and GPB); polymorphism between M and N antigens on GPA is attributed to amino-acid substitutions at residues 1 (Ser/Leu) and 5 (Gly/Glu), but the N-terminal Ser^1 and Leu^1 are the primary determinants for the M and N antigens respectively. GPB carries 'N' (N-like activity), S/s, and U blood-group antigens; 'N' activity resides at the N terminus of GPB, the sequences of GPA and GPB between residues 1 and 26 being identical; the S/s antigenic determinants arise from Met/Thr polymorphism at residue 29 of GPB; and the U antigen, present in all Caucasians and most Blacks, resides between residues 33 and 39.

Mo *symbol for* molybdenum.

mob the genetic notation for genes involved in the mobilization of a **plasmid** from cell to cell.

mobile element *an alternative term for* **transposon**.

mobile phase the phase that moves in a chromatographic system; it can include the portion of the starting sample present in this phase at any given time.

mobility **1** the property of being mobile. **2** *see* **electrophoretic mobility**.

mobilization *or* **mobilisation** **1** the act or process of mobilizing. **2** the process by which a conjugative plasmid brings about the transfer from one cell to another of DNA to which it is not stably and covalently linked.

mobilize *or* **mobilise** to bring (resources or reserves) into use for a particular purpose, e.g. to mobilize fat by lipolysis or glycogen by glycogenolysis.

mobilizing plasmid *or* **mobilising plasmid** *an alternative name for* **conjugative plasmid**.

Möbius strip *or* **Moebius strip** any one-sided continuous surface with a single bounding curve made by twisting a ribbon through 180° and joining the ends together. When divided lengthwise it forms another Möbius strip of double the length, and is a model for the replicative behaviour of a circular chromosome that contains a single twist. [After its inventor, August Ferdinand Möbius (1790–1868), German mathematician.]

Mo cell a relatively small cell, containing round, osmophilic granules, that is believed to produce **motilin**. Mo cells occur in the upper small intestine of humans, mainly in the crypts; they are sparse in the lower small intestine.

modal class *(in a statistical distribution)* the class that contains the **mode** (def. 2).

mode **1** any particular way or manner of existing or of doing something. **2** *(in a statistical distribution)* the value of the variable occurring with greatest frequency. **3** any of the sev-

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eral wave frequencies that an oscillator can generate, or to which a resonator can be tuned to respond. —**modal** *adj.*; **modality** *n.*

modeccin a 57 kDa lectin present in the turnip-like root of the southern African plant, *Modecca digitata*. It is highly toxic to animals, its prime action being on the liver, and to animal cells in culture. It consists of two polypeptide subunits in disulfide linkage, the A (smaller) subunit being biologically indistinguishable from the A subunits of ricin and abrin. *See also* **ribosome-inactivating protein**.

model **1** a three-dimensional representation of an object, structure, etc., sized to be conveniently seen, handled, and studied. **2** a conceptual representation of a particular phenomenon, system, or set of experimental observations as an aid to understanding and as an object for test or for further experimentation. **3** an animal that, often as a result of mutation, mimics a pathological condition and can be used to study the pathogenesis of the condition. *See also* **transgenic**. **4** a mathematical representation of a particular phenomenon, system, or set of experimental observations as an aid to calculation and prediction. **5** to construct or create a **model** (def. 1, 2, 3). —**modelled** *or (sometimes US)* **modeled** *adj.*; —**modelling** *or (sometimes US)* **modeling** *n.*

model system any biological or biochemical system that is used for study because it is considered to be representative of one or more other (often more complex) systems in which similar phenomena occur or are believed to occur.

modem an electronic device, consisting of a combined modulator and demodulator, that is used to convert an output signal from one type of equipment (e.g. a computer) into a form suitable for input into another type, and vice versa. [From modulator–demodulator.]

moderator any substance that changes the rate of an enzymic or other reaction, either positively or negatively.

modification **1** *(in biochemistry) see* **covalent modification**. **2** *(in genetics)* any nonheritable change in the phenotype of an organism in response to variation of its environment; it includes **host-controlled modification**. *Compare* **mutation**.

modification enzyme any enzyme that effects **covalent modification**. *See also* **restriction–modification system**.

modification gene *see* **restriction–modification system**.

modification methylase *a common name for* any of the enzymes that methylate specific sites on a DNA molecule.

modification–restriction system *an alternative name for* **restriction–modification system**.

modifier *an alternative term for* **effector**.

modifier gene *or* **modifying gene** any gene that affects the phenotypic expression of a gene or genes at other loci.

modify **1** to alter the structure, character, activity, etc. of (something). **2** to convert a chemical compound into an analogue, especially by substitution. *See also* **modification**.

modular primer an unligated tandem arrangement of **primers** (usually two or three) used for the **polymerase chain reaction** and related experiments.

modulating codon any codon that controls the frequency with which a **cistron** or cistrons are transcribed.

modulation **1** adjustment or regulation of the degree or activity of something. **2** regulation of the frequency with which a **cistron** or cistrons is transcribed. **3** control of the activity of a regulatory enzyme by an effector. **4** *(in physics)* the process of changing the amplitude, frequency, or phase of a wave by combination with another wave.

modulator **1** something that modulates or brings about modulation. **2** any molecule that acts as an **effector**. **3** *(in pharmacology)* a ligand that increases or decreases the action of an agonist by combining with a distinct (allosteric) site on the receptor macromolecule.

modulator protein *one provisional name for* **calmodulin**.

module a standardized or self-contained part or unit of construction, especially one that can be used in alternative combinations with others; e.g. one of a set of such assemblies of electronic components that comprise a larger piece of equipment. *See also* **Appendix E.** —**modular** *adj.*

moesin *abbr. for* membrane-organizing extension spike protein; a protein, isolated from bovine uteri, with one domain similar to one in **ezrin**, band 4.1, and related proteins. Moesin occurs in many cell types and tissues and is involved in connections of major cytoskeletal structures to the plasma membrane. Example from human: database code MOES_HUMAN, 576 amino acids (67.61 kDa).

Moffitt–Yang equation *or* **Moffitt equation** a phenomenological equation, related to the **Drude equation**, that describes the anomalous variation of optical rotatory dispersion with wavelength shown by polypeptides containing helical sections. It is used to provide an estimate of the alpha-helical content of polypeptides and proteins. If λ is the wavelength of observation and $[m']_\lambda$ is the reduced **mean residue rotation** at that wavelength,

$$[m']_\lambda = \{a_0\lambda_0^2/(\lambda^2 - \lambda_0^2)\} + \{b_0\lambda_0^4/(\lambda^2 - \lambda_0^2)^2\},$$

where a_0, b_0, and λ_0 are empirical constants; a_0 is a function of contributions to the optical rotation from both the helix and the residue side-chains, as well as from the solvent, and b_0 and λ_0 are related principally to the amount of helical structure in the molecule. A value of λ_0 is chosen to give the best straight line when $[m'](\lambda^2 - \lambda_0^2)$ is plotted against $1/(\lambda^2 - \lambda_0^2)$, a good fit usually being obtained if λ_0 = 212 nm when λ = 350–600 nm. The slope of this line, $b_0\lambda_0^4$, gives a value of b_0, whence by reference to the values found for nonhelical and fully helical synthetic polypeptides an estimate may be made of the alpha-helical content of a polypeptide or protein under investigation. [After William E. Moffitt (1925–58), British physical chemist and Jen Tsi Yang (1922–95), who formulated it in 1956.]

Mohr pipette a cylindrical pipette calibrated for delivery from the zero mark to a particular chosen graduation mark. [After Carl Friedrich Mohr (1806–1879), German chemist.]

Mohr's salt ammonium ferrous sulfate; di-ammonium iron(II) sulfate hexahydrate; $(NH_4)_2SO_4{\cdot}FeSO_4{\cdot}6H_2O$.

moiety either of two, usually distinctive, component parts of a complex molecule; e.g. the steroid and saccharide moieties of a cardiac glycoside.

mol *symbol for* mole.

mol. *abbr. for* **1** molecular. **2** molecule.

μmol *symbol for* micromole.

molal **1** denoting the concentration of a solute (or a solution as a whole) expressed as the amount of substance of the solute divided by the mass of solvent. It is measured in moles per kilogram. **2** denoting an amount-of-substance **concentration** measured in such terms. *Compare* **molar**.

molality *symbol: m or b*; a measure of concentration expressed as the number of moles (of a specified solute) per kilogram of solvent. Molality is independent of temperature. *See also* **molal**.

molar **1** denoting an extensive physical quantity that is measured per mole (of a specified substance). It is usually denoted by the subscript m in the symbol; e.g. **molar volume** is the volume of one mole of a substance, and the symbol is V_m. *Compare* **specific**. **2** denoting an intensive physical quantity that is measured per mole (of a specified substance); i.e. divided by concentration. Use of the term molar in this sense is no longer recommended, except in the terms **molar absorption coefficient** and **molar conductivity**. **3** denoting the concentration of a solute (or a solution as a whole), expressed as the amount of substance of the solute divided by the mass of the solution. The recommended units are moles per litre but the convenient symbols M and M are frequently used. *Compare* **molal**.

molar absorbancy index *a former name for* **molar absorption coefficient**.

molar absorption coefficient either the **molar decadic absorption coefficient** (*symbol*: ε) or the **molar Napierian absorption coefficient** (*symbol*: κ); these are, respectively, the decadic **absorbance** or the Napierian absorbance of a substance, or of a

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solute in solution, (at a specified wavelength (or frequency) and temperature) divided by the optical path length (in cm) of the medium and by the amount-of-substance concentration of the substance; i.e. the decadic or Napierian absorption coefficients of a medium whose concentration is expressed in moles per litre. *Former names*: molar absorbancy index; molar absorptivity; molar extinction coefficient; molecular extinction coefficient. *See also* **absorption coefficient**.

molar absorptivity *a former name for* **molar absorption coefficient**.

molar activity an **activity** (def. 1) of a substance or material divided by its amount of substance (in moles). *Compare* **specific activity**.

molar catalytic activity the **catalytic activity** of an enzyme, under specified conditions, divided by the amount of substance (in moles), either of enzyme catalytic centres or of multi-centre molecules; in the latter case it is important to specify whether the measurements refer to catalytic centres or to molecules. It may be expressed in katals per mole of enzyme. If the conditions specified are such that the enzyme is saturated with substrate, the expression (which then replaces the obsolete term turnover number) will be numerically equal to the **catalytic constant**, in s^{-1}, for decomposition of the enzyme–substrate complex into enzyme and products, although its interpretation may be complex. *Compare* **molar enzymic activity**, **specific catalytic activity**.

molar concentration *an old but now incorrect term for* **amount-of-substance concentration** measured in moles per litre. *See* **molar** (def. 2).

molar conductivity *symbol*: Λ ;the **electrolytic conductivity** of a (specified) electrolyte divided by its amount-of-substance concentration. The SI derived unit is the S m^2 mol^{-1}.

molar decadic absorption coefficient *symbol*: ε; *see* **molar absorption coefficient**.

molar ellipticity *or (formerly)* **molecular ellipticity** *symbol*: $[\Theta]$; an expression of circular dichroism, $\Delta\varepsilon$, at a specified wavelength, λ. It is given by the relation: $[\Theta]_\lambda = 3299\ \Delta\varepsilon_\lambda$.

molar enzymic activity *(obsolete)* the phenomenological coefficient relating the **enzymic activity** (under specified conditions) to the molar amount of enzyme substance; it is expressed in katals per mole of enzyme. It has now been superseded by **molar catalytic activity**.

molar extinction coefficient *a former name for* **molar absorption coefficient**.

molarity *an older (still widely used) term for* **amount-of-substance concentration** expressed in mol dm^{-3} or mol L^{-1}. *See* **concentration** (def. 1b), **molar** (def. 3).

molar mass the mass of a substance divided by its **amount of substance**; it is commonly expressed in grams (sometimes kilograms) per mole. *Compare* **molecular mass**, **relative molecular mass**.

molar Napierian absorption coeffient *symbol*: κ; *see* **molar absorption coefficient**.

molar optical rotation *symbol*: $[m]$ *or* $[M]$; the observed optical rotation, α_{obs}, of a substance, or of a solute in solution, (at a specified wavelength (or frequency) and temperature) divided by the optical path length (in dm), l, of the medium and by its amount-of-substance concentration (in mol dm^{-3}), c. It is given by:

$$[m] = \alpha_{obs}/cl = [\alpha]^\theta_\lambda M_r/100$$

in deg dm^2 g^{-1}, where $[\alpha]^\theta_\lambda$ is the **specific optical rotation**.

molar optical rotatory power *symbol*: α_m; it is given by the relation $\alpha_m = \alpha/cl$ in rad m^2 mol^{-1}, where α is the observed rotation in radians, c is the amount-of-substance concentration in mol dm^{-3}, and l is the optical path length of the sample in m. *See also* **specific optical rotatory power**.

molar volume *symbol*: V_m; the volume occupied by a substance, under specified conditions of temperature and pressure, divided by its **amount of substance**; it is commonly expressed in litres per mole.

mold *the US spelling of* **mould**.

mole *symbol*: mol; the SI base unit of **amount of substance**, defined as the amount of substance of a system that contains as many elementary entities as there are atoms in 0.012 kilogram of carbon-12; the elementary entities must be specified and may be atoms, molecules, ions, electrons, other particles, or specified groups of such particles. One mole of a compound has a mass equal to its **relative molecular mass** in grams.

molecular **1** of or pertaining to a molecule or molecules. **2** consisting of or existing as molecules; (especially of certain gaseous elements) present or reacting as intact molecules rather than as atoms, ions, etc., e.g. molecular oxygen (i.e. dioxygen). **3** of dimensions comparable to those of molecules. **4** *(in physical chemistry) an obsolete term meaning* divided by molecular weight or expressed per gram-molecule; **molar** now used. **5** considered in terms of or at the level of molecules, or in terms of chemical substances or structures and their interconversions; e.g. molecular biology, molecular medicine.

+molecular *comb. form* indicating the **molecularity** of a chemical reaction (when qualified by a multiplicative prefix), e.g. unimolecular, bimolecular, termolecular.

molecular biology the science that strives to understand the chemical and physical basis of biological specificity and variation, especially with regard to the structure, replication, and expression of genes, and to the structure, interaction, and physiological function of gene products. —**molecular biologist** *n.*

molecular chaperone *see* **chaperone**.

molecular cloning *or* **DNA cloning** the isolation in a bacterial cell of a fragment of any heterologous DNA in covalent linkage with a replicon (plasmid, phage, etc.) in order to obtain a homogeneous population (i.e. clone) of DNA molecules from the progeny of such a cell. The DNA to be cloned may be a fragment of genomic DNA obtained by restriction endonuclease digestion, or a complementary DNA (cDNA). The foreign DNA is inserted into the **cloning vector** which has been cleaved with a restriction enzyme; the gaps between vector and insert DNA are sealed with DNA ligase. In cloning using plasmid vectors, plasmids are then reintroduced into host cells by **transformation**; markers on the cloning vector allow selection of plasmid-containing cells and identification of those cells that contain recombinant plasmids (rather than 'empty' vectors). To identify clones containing particular sequences, DNA from individual colonies may be screened with a labelled DNA probe by **colony hybridization**. In cloning using bacteriophage vectors, the ligated insert and vector are packaged into phage capsids *in vitro,* and then these are used to infect host bacteria.

molecular disease any disease caused by an abnormality in a single protein, usually an enzyme. This component may have an abnormal structure that makes it functionally less efficient or harmful to the organism, or it may have a normal structure but be present in reduced amount. An example is **sickle-cell anemia**. Overproduction of proteins, e.g. of oncogene products, may also lead to a pathological situation.

molecular distillation distillation at very low pressures (at or below 1.3 N m^{-2}) when the mean free path of the molecules is of the same order as the distance between the surface of the liquid being distilled and the distillate; the molecules can therefore travel rapidly from the liquid to the distillate with relatively few collisions, and with a reduced risk of thermal denaturation or decomposition. The technique is useful in the separation and purification of fat-soluble vitamins and other natural products.

molecular dynamics the study of the relative intramolecular differences in the motions of the components of (macro)molecules.

molecular ellipticity *a former term for* **molar ellipticity**.

molecular endocrinology endocrinology at the molecular level.

molecular entity any chemically or isotopically distinct atom, molecule, ion, ion pair, radical, radical ion, complex, con-

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former, etc., capable of existence as a separately distinguishable entity.

molecular enzymology *(sometimes)* the aspects of enzymology concerned with kinetics and mechanisms.

molecular exclusion chromatography *a less common name for* **gel-permeation chromatography**.

molecular extinction coefficient *a former name for* **molar absorption coefficient**.

molecular formula a chemical formula giving the kinds and number of atoms in one molecule of a specified substance.

molecular fragmentography *an alternative (less satisfactory) name for* **selected-ion monitoring**.

molecular genetics the branch of genetics that attempts to describe genetic events in molecular terms.

molecular graphics *functioning as sing.* the use of computer programs for visualizing (macro)molecules, refining structures and molecular design, protein engineering, etc. Suites of programs that are commonly used include Insight, Ribbons, Midas, and O.

molecular hybridization *an alternative name for* **hybridization analysis**.

molecular ion any ion produced, especially in a mass spectrometer, when a molecule loses or gains an electron, forming a molecular cation or molecular anion, respectively.

molecularity the number of molecular entities involved in a simple, one-step, chemical reaction (it is not used to describe an overall reaction with more than one step). In the two-step reaction: $A + B \rightarrow C \rightarrow D$, the molecularity of the first step is two, i.e. it is bimolecular, and the molecularity of the second step is one, i.e. it is unimolecular.

molecular mass the mass of one molecule of a specified substance expressed in (unified) atomic mass units or daltons. *Compare* **relative molecular mass**, **molecular weight**.

molecular matchmaker any of a class of proteins, also called matchmaker proteins, that cause a conformational change in one or both components of a DNA–protein binding pair to promote formation of a metastable DNA–protein complex. ATP hydrolysis occurs in the process. Such matchmaking is used extensively in repair, replication, and transcription of DNA.

molecular medicine *(sometimes)* the branch of medicine concerned with the biochemical mechanisms of disease processes and therapy.

molecular orbital a wave equation for one electron describing its movement in the effective field provided by the nuclei and all other electrons of a molecular entity of more than one atom.

molecular pathology the use of techniques of molecular biology to enhance the understanding, diagnosis, and therapy of disease (mainly with respect to humans).

molecular pharmacology the use of techniques of molecular biology to enhance the understanding of the mechanism of action of existing drugs, and with the help of molecular graphics to predict the structure of novel drugs, especially compounds that might bind to proteins of known structure.

molecular p*K* any one of the **p*K*** values of an acid with two or more dissociations. *Compare* **group p*K***, **titration p*K***.

molecular recognition the specific **recognition** of one molecule by another; it often includes **chiral recognition**.

molecular ruler **1** any rigid oligoproline crosslinking reagent of defined length. Such reagents are useful in probing the structures of biological macromolecules in solution. **2** any molecule that regulates length, e.g. **nebulin**.

molecular sieve any of a class of substances or materials, whether naturally occurring or artificial, that contain pores of molecular dimensions and of a closely defined range of diameters. They are useful for the separation of substances within a particular range of molecular dimensions on the basis of selective exclusion.

molecular-sieve chromatography any form of chromatography in which a separation is based mainly upon differences in molecular size and/or shape of the substances being separated. It includes **gel-permeation chromatography** and separations using **zeolites**.

molecular-sieve electrophoresis *(sometimes) an alternative term for* **polyacrylamide gel electrophoresis**.

molecular weight *abbr.*: mol. wt. *or* M.W.; *a former name for* **relative molecular mass**.

molecular weight cut-off *or* **cut-off** *a jargon term for* the nominal maximal value of the relative molecular mass of a macrosolute that can pass through an ultrafiltration membrane of a particular grade.

molecular weight marker *or* **molecular weight standard** a *jargon term for* any soluble polymer of accurately known relative molecular mass that serves as a reference in estimations of M_r values of polymers by techniques such as gel permeation chromatography or gel electrophoresis. Generally a set of such substances, covering a range of M_r values, is used.

molecule a structural unit of matter consisting of one or more atoms; the smallest discrete part of a specified element or compound that retains its chemical identity and exhibits all its chemical properties.

mole fraction *an alternative name for* amount-of-substance fraction. *See* **concentration**.

mole percent the quantity mole fraction multiplied by 10^{-2}; usage no longer recommended.

Molisch test a qualitative test for free or combined aldohexoses. It depends on the formation of a purple colour when the furfural derivatives, formed when aldohexoses are heated with strong acids (e.g. H_2SO_4), react with sulfonated 1-naphthol. [After Hans Molisch (1856–1937), Austrian chemist.]

mollicute *see* **mycoplasma**.

molt *the US spelling of* **moult**.

molting hormone *the US spelling of* moulting hormone (i.e. **ecdysterone**).

mol. wt. *abbr. for* molecular weight (alternative to M.W.).

molybdate **1** the bivalent anion, MoO_4^{2-}, derived from molybdic acid. **2** any salt of molybdic acid.

molybdenum *symbol*: Mo; a metallic transition element of group 6 of the (IUPAC) **periodic table**; atomic number 42; relative atomic mass 95.94. It consists of a mixture of eight stable nuclides of which the commonest is that of mass number 98. It forms molybdates (molybdenum(VI)) and can also exist in various lower oxidation states. Molybdenum is of low abundance in the Earth's crust and is an essential trace component of living material, where it participates in numerous redox reactions. It is a constituent of component I (or molybdoferredoxin) of the **nitrogenase** (EC 1.18.6.1) complex from legume nodule bacteria (bacteroids), which converts nitrogen into ammonia. There are many artificial radionuclides of molybdenum, of which the most widely used is molybdenum-99.

molybdo+ *comb. form* denoting containing molybdenum, e.g. molybdoprotein.

molybdoferredoxin *an alternative name for* component I of **nitrogenase**.

molybdophosphoric acid *or* **phosphomolybdic acid** a heteropolyacid of approximate formula $24MoO_3 \cdot P_2O_5 \cdot xH_2O$, where x is approximately 50. It is useful in reagents for alkaloids, xanthine, uric acid, creatinine, etc.

mon+ *a variant form of* **mono+** (sometimes before a vowel).

Mon *symbol for* the montanoyl group.

monactin *see* **nonactin**.

monatomic *or* **monoatomic** (of a molecular entity) composed of only one atom.

monellin an ≈11 kDa protein consisting of two polypeptide chains of the same size but different sequence, linked noncovalently, isolated from the fresh fruits of the African shrub *Dioscoreophyllum cumminsii*, known as serendipity berry. It is intensely sweet-tasting, being 3000 times sweeter than sucrose on a mass basis, and has sequence similarities with **thaumatin**. A chain: database code MONA_DIOCU, 50 amino acids (5.83 kDa); B chain: database code MONB_DIOCU, 50 amino acids (5.83 kDa).

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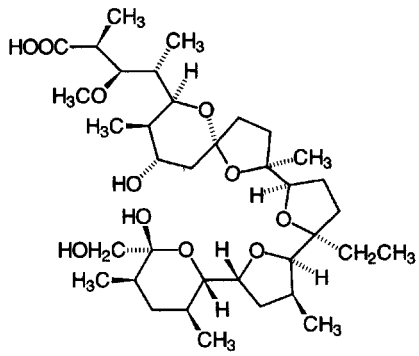
monensin a 671 Da, open-chain macrotetrolide-like antibiotic, with many chiral centres, isolated from *Streptomyces cinnamonensis*. It forms stable complexes with monovalent cations, especially with Na^+, and exhibits high Na^+/K^+ selectivity. These complexes are soluble in organic solvents and thus monensin can act as an **ionophore** for monovalent cations. It is used as a digestion-modifying feed additive in ruminants.



Monera the kingdom containing all prokaryotic organisms (i.e. bacteria and cyanobacteria) in the five-kingdom system of classification. —**moneran** *adj., n.*

mongolism *an older name for* **Down's syndrome**.

monitor **1** any instrument or device for checking, controlling, measuring, or keeping a record of some varying biological activity or chemical or physical property, e.g. absorbance, (radio)activity, concentration, pH, respiration. **2** to serve as a monitor of (some activity or property); to use a monitor.

mono+ *or (sometimes before a vowel)* **mon+** *comb. form* **1** denoting one, single, onefold, once, alone; **uni+**. **2** *(in adjectives describing physical attributes)* homogeneous; e.g. monochromatic, monodisperse, monoenergetic. **3** *(in generic names of chemical compounds)* denoting that member of a series (a) having only one specified substituent or other chemical modification, e.g. monoacylglycerol, monoamine; or (b) comprised of only one constitutional unit, e.g. monomer, monosaccharide. **4** *informal term (in specific names of chemical compounds)* indicating or emphasizing the presence in a molecule of a single specified atom, group, or residue; e.g. monoiodotyrosine, adenosine monophosphate, monosodium dihydrogen phosphate. **5** *(in adjectives describing compounds or substances)* having a single function of the kind specified; e.g. monoacidic, monobasic, monodentate, monohydric. **6** *(in names of processes or enzymes)* concerned with or acting on, one or only one chemical group of the kind specified; e.g. monoiodination, monoesterase.

monoacidic (of a **base** (def. 1)) able to accept only one proton per molecule in solution.

monoacylglycerol *or (formerly)* **monoglyceride** any ester of glycerol in which any one of its hydroxyl groups has been acylated with a fatty acid, the other being non-esterified.

monoacylglycerol pathway a pathway in which diacylglycerols and triacylglycerols are formed by sequential acylation of monoacylglycerol by acyl-CoA. It was initially studied especially in cells of mammalian intestine, and is important during fat absorption since monoacylglycerol is then extensively absorbed from the gut; however, it is also present in a large number of other mammalian tissues. There is little evidence for this pathway in plants.

monoamine oxidase *abbr.*: MAO; *a common name for* amine oxidase (flavin-containing), EC 1.4.3.4; an enzyme, widely distributed in animal tissues, that catalyses the oxidative deamination of primary amines by a reaction between dioxygen and $R–CH_2–NH_2$ to form R–CHO, NH_3, and H_2O_2. It also acts on secondary and tertiary amines. It is important in the catabolism of neuroactive amines, e.g. epinephrine, norepinephrine, serotonin (5-hydroxytryptamine), and tyramine. Example from *Rattus norvegicus*: database code AOFA_RAT, 526 amino acids (59.51 kDa).

monoamine oxidase inhibitors compounds that inhibit **monoamine oxidase** (*abbr.*: MAO) and are useful as thymoleptic (antidepressant) drugs. They act by increasing the concentrations of **norepinephrine** and **serotonin**, which, because of the block on their metabolism, accumulate in the synaptic gap and exert an increased postsynaptic effect. They were discovered as a result of the observation of the euphoric side effect of the antitubercular drug **isoniazid**. The main groups of these drugs are (1) the **cyclopropylamines**, including tranylcypromine (*trans*-phenyl-cyclopropylamine); and (2) the **propargylamines**, including pargyline (*N*-benzyl-*N*-methyl-2-propynylamine. **Harmine** and related carboline alkaloids are reversible MAO inhibitors but are not used therapeutically.

monoatomic *a variant spelling of* **monatomic**.

monobactam any of a family of *N*-sulfonated monocyclic β-lactam antibiotics produced by a range of bacterial species.

monobasic **1** (of an acid) able to yield only one hydrogen ion per molecule in solution. **2** (of a salt or ester of a polybasic acid) derived by the replacement of only one of its dissociable hydrogen atoms per molecule.

monochromatic **1** *or* **homochromatic** involving, possessing, or relating to a single colour; consisting of, relating to, or emitting light (or other electromagnetic radiation) of a single frequency or wavelength. **2** *an alternative term for* **monoenergetic**. *Compare* **heterochromatic** (def. 1), **polychromatic**.

monochromator a device used for producing light (or other electromagnetic radiation) of essentially one frequency or wavelength, which may be fixed or selectable.

monocistronic containing as much genetic information as is contained in a single **cistron**.

monocistronic messenger RNA any messenger RNA molecule that carries one initiation site only and encodes the synthesis of one polypeptide chain only. It is characteristic of eukaryotes, which do not possess **polycistronic messenger RNA**.

monoclonal **1** of, pertaining to, being, formed by, or derived from a single **clone** (def. 1). **2** *(sometimes) an informal name for* **monoclonal antibody**.

monoclonal antibody *or (sometimes, informal)* **monoclonal** an immunoglobulin secreted by a single clone of antibody-producing cells, either *in vivo* or in culture. Such antibodies are **monospecific;** they can thus be useful as immunochemical reagents for the detection or assay of particular antigens. *See also* **hybridoma**.

monocomponent insulin a commercial preparation of natural insulin that has been highly purified by chromatography and is thus made essentially free of proinsulin, intermediates in the conversion of proinsulin to insulin, and breakdown products of insulin, as well as any unrelated contaminants.

monocotyledon *or* **monocot** any flowering plant having a single cotyledon (seed leaf) in the embryo. Such plants comprise the class Monocotyledonae.

monocyclic having a single ring of atoms in the molecule.

monocyte a large leukocyte of the **mononuclear phagocyte system**, 16–22 μm in diameter (in humans), with pale-staining cytoplasm and a reniform or horseshoe-shaped nucleus. Found in bone marrow and the bloodstream, monocytes are derived from pluripotent stem cells and become macrophages when they enter the tissues.

Monod, Jacques Lucien (1910–76), French microbiologist and molecular biologist; Nobel Laureate in Physiology or Medicine (1965) jointly with F. Jacob and A. M. Lwoff 'for their discoveries concerning genetic control of enzyme and virus synthesis'.

monodisperse describing a colloidal system in which the dispersed phase consists of particles all of (nearly) the same size. —**monodispersity** *n.*

Monod–Wyman–Changeux model (for allosteric interactions)

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abbr.: MWC model; a model describing the nature of **allosteric** interactions in proteins. It requires an allosteric protein to be an oligomer, the protomers of which are associated in such a way that they all occupy equivalent positions. Each protomer has only one stereospecific binding site for each ligand. The protein can exist in either of two conformational states, the T form (**tense form**), the predominant form when unligated, and the R form (**relaxed form**); these states are in equilibrium. The affinity of the R form for ligand is higher than that of the T form. All binding sites in each state are deemed to be equivalent and to have identical dissociation constants, K_R and K_T for the R and T forms, respectively. The sigmoidal binding curve for any allosteric protein and a given ligand can be calculated from the allosteric constant, L, equal to the ratio [T form]/[R form] for the unligated states and the two dissociation constants. [After J. **Monod**, Jeffries Wyman (1901–95), US biochemist, and Jean-Pierre Changeux (1936–), French biochemist.] *See also* **mnemonic enzyme mechanism**.

monoenergetic *or* **monochromatic** (of moving particles and sometimes also photons) all having the same kinetic energy.

monoenoic denoting any alkenyl carboxylic acid containing one carbon–carbon double bond per molecule.

monoester any simple ester; i.e. any **ester** formed by condensation of one molecular proportion of an alcohol or phenol with one of an oxoacid.

monoesterase *see* **phosphomonoesterase**.

monofunctional having only one function or one reactive chemical group.

monoglyceride *a former name for* **monoacylglycerol**; its use is discouraged as it does not convey the intended meaning.

monognotobiotic *an alternative term for* **axenic**.

monohydric *or* **monohydroxy** describing any chemical compound containing one hydroxyl group per molecule. It is used especially of alcohols.

monoiodinated reacted with or containing only one atom of iodine per molecule.

monokine *an alternative name for* a **cytokine** produced by monocytes.

monolayer **1** *an alternative name for* **monomolecular layer**. **2** a single layer of cells grown or growing in culture.

monomer **1** any substance that can provide one or more (in number or species) of the monomeric units of an **oligomer** (def. 1) or of a **polymer** (def. 1); a molecule of such a substance. **2** *a loose term for* any of the component molecules (identical or nonidentical) formed by the complete dissociation of a macromolecule with quaternary structure. **3** *(in molecular biology)* **a** any protein that is made up of nonidentical structural units. **b** any of the structural units formed by dissociation of an oligomeric protein and corresponding to a **protomer** in the undissociated protein. —**monomeric** *adj.*

monomeric unit a group of atoms, derived from a molecule of a given **monomer** (def. 1), that comprises any one species of constitutional unit of a polymer.

monomolecular **1** relating to, consisting of, or involving a singular **molecular entity**. **2** (of a reaction) having a **molecularity** of one; unimolecular.

monomolecular layer *or* **monolayer** a layer of a substance or substances that is one molecule thick.

mononuclear **1** (of a cell) having one nucleus. **2** (of a metal-ion–ligand complex) containing a single central metal atom.

mononuclear phagocyte system a cell system in higher animals that comprehends all the highly phagocytic mononuclear cells and their precursors. As well as the free macrophages, it includes precursor cells and promonocytes of the bone marrow, monocytes of the bone marrow and the blood, and the tissue macrophages. The term has been proposed as a replacement for **reticuloendothelial system**, now held to lack precision.

mononucleosis *see* **Epstein–Barr virus**.

mononucleotide any **nucleotide** (def. 1); the term is used especially as the generic name of the constitutional repeating unit of all oligonucleotides, polynucleotides, and nucleic acids. A mononucleotide consists of the (3′- or 5′-)phosphate of a single ribonucleoside or deoxyribonucleoside. The term is extended generally to include: (1) nucleoside oligophosphates, e.g. adenosine 5′-triphosphate (ATP); (2) nucleoside diphosphate sugars, e.g. uridine 5′-diphosphate glucose (UDPG); (3) nucleoside 2′,3′- and 3′,5′-(cyclic)phosphates, e.g. adenosine 3′,5′-phosphate (cyclic AMP); (4) nucleoside phosphates derived from artificial heterocyclic bases, e.g. 5-iodo-2′-deoxycytidine 5′-triphosphate, or from ones that do not occur naturally in nucleic acids, e.g. inosine 5′-phosphate (i.e. inosinic acid; hypoxanthine riboside 5′-phosphate; IMP); and (5) certain analogous compounds such as those containing, in place of a residue of ribose or deoxyribose, a residue of ribitol, e.g. flavin mononucleotide (i.e. riboflavin 5′-phosphate; FMN), of dideoxyribose, e.g. 2′,3′-dideoxyadenosine 5′-triphosphate (i.e. ddATP), or of another pentose, e.g. cytosine arabinoside 5′-triphosphate (i.e. *ara*-CTP). *Compare* **oligonucleotide**, **polynucleotide**.

monooxygenase any oxidoreductase enzyme that brings about the incorporation of only one atom of oxygen from dioxygen into the donor; such enzymes catalyse reactions of the type:

$$\text{substrate} + O_2 = \text{oxidized substrate} + H_2O \ (+ CO_2 \text{ in many cases}).$$

The following are examples. (1) Lysine 2-monooxygenase; EC 1.13.12.2; it catalyses the oxidation by dioxygen of L-lysine to 5-aminopentanamide, CO_2, and H_2O; FAD is a coenzyme. (2) Lysine 6-monooxygenase; EC 1.13.12.10; it catalyses the oxidation by dioxygen of L-lysine to N^6-hydroxy-L-lysine and H_2O. (3) Tryptophan 2-monooxygenase; EC 1.13.12.3; it catalyses the oxidation by dioxygen of L-tryptophan to indole-3-acetamide, CO_2, and H_2O. (4) *myo*-Inositol oxygenase; EC 1.13.99.1; it catalyses the oxidation by dioxygen of *myo*-inositol to D-glucuronate and H_2O; iron is a cofactor. (5) Phenol 2-monooxygenase; EC 1.14.13.7; *other name*: phenol hydroxylase; it catalyses a reaction between phenol, NADPH, and O_2 to form catechol, $NADP^+$, and H_2O; FAD is a coenzyme. It is an enzyme of bacterial aromatic substrate utilization; example from *Pseudomonas pickettii*: database code: TBUD_PSEPI, 670 amino acids (72.79 kDa). (6) *trans*-Cinnamate 4-monooxygenase; EC 1.14.13.11; *other names*: cinnamic acid 4-hydroxylase; cinnamate 4-hydroxylase; CA4H; it catalyses a reaction between *trans*-cinnamate, NADPH, and O_2 to form 4-hydroxycinnamate, $NADP^+$, and H_2O. It is a cytochrome P450–thiolate enzyme; example from Jerusalem artichoke: database code: TCMO_HELTU, 505 amino acids (57.85 kDa). *See also* **monophenol monooxygenase**.

monophenol monooxygenase EC 1.14.18.1; *other names*: tyrosinase; phenolase; monophenol oxidase; cresolase. An enzyme involved in the formation of melanins and other polyphenolic pigments, etc. It catalyses a reaction between L-tyrosine, L-dopa, and O_2 to form L-dopa, dopaquinone, and H_2O; copper is a cofactor. It has four motifs, three for the Cu site. Example from human (precursor): TYRO_HUMAN, 529 amino acids (60.33 kDa). Deficiency results in **albinism**.

monophosphatidyl glycerol any [1,2-diacyl-*sn*-glycero-3-(phospho-1-*sn*-glycerol)] lipid present in chloroplasts of higher plants.

monoploid (of cells or individuals) having a single set of chromosomes; i.e. in a polyploid series, having the fundamental **haploid** chromosome number; true haploid.

monosaccharide *the generic name of* the simplest carbohydrates. Monosaccharides cannot be hydrolysed to give smaller carbohydrates. They are polyhydric alcohols containing either (in **aldoses**) an aldehyde group or (in **ketoses**) a keto group and with from three to ten or more carbon atoms. Monosaccharides form the constitutional repeating units of oligo- and polysaccharides. The names and structures of the common aldoses (from triose to hexose) form the basis for prefixes used to describe other compounds containing a set of

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>CHOH groups. For structures, see illustration (note that if X = CHO and Y = CH_2OH these structures also depict the common D aldoses.) An example of prefix use is the ketoheptonic acid phosphate, DAHP, **3-deoxy-D-*arabino*-(2)-heptulosonate 7-phosphate**. By extension the stereochemical relationships are applied to substituents other than OH, e.g. in **threonine**. *See also* **glycose** (def. 1), **heptose**, **hexose**, **pentose**, **tetrose**, **triose**.

monose *an obsolete term for* **monosaccharide**.

monosodium glutamate *abbr.*: MSG; the monosodium salt of L-glutamic acid, widely used as a flavouring agent for its meaty taste, and the most active component of soy sauce. Consumption by adults of more than about 3.0 g can cause **Chinese restaurant syndrome**, characterized by a feeling of tightness, facial pressure, burning sensation, and headache. The D-enantiomer does not have the characteristic taste and up to 7.0 g can be consumed without ill effect.

monosome **1** any chromosome in a functionally diploid chromosome set that lacks a homologue. **2** a structure consisting of a single ribosome bound to a molecule of messenger RNA.

monosomic (of cells, tissues, or individuals) having one or more **monosomes** (def. 1).

monospecific (of an antibody or an antiserum) only able to react with a single specified antigen or antigenic determinant.

monoterpene any **terpene** containing or derived from two isoprene units and thus containing ten carbon atoms. Monoterpenes may be acyclic or mono- or dicyclic.

monotonic (of a mathematical function) varying in such a manner that it continuously either increases or decreases as the independent variable increases. —**monotonically** *adv.*

monotopic describing a protein molecule that does not cross a cellular membrane.

monovalent *an alternative term for* **univalent**.

monoxenic *see* **synxenic**.

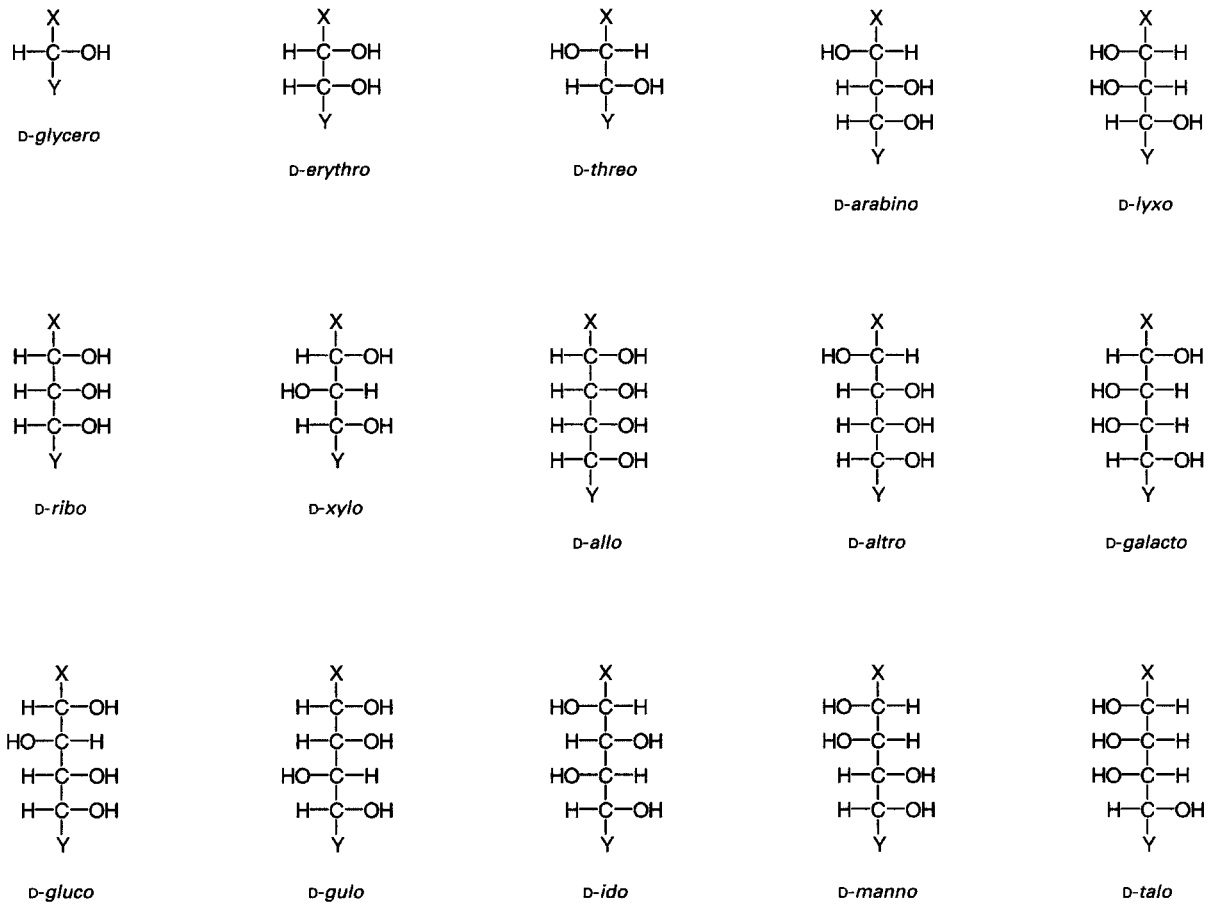
monozygotic **1** (of twins, triplets, etc.) derived from a single fertilized ovum. **2** any one of a set of monozygotic individuals. *Compare* **dizygotic**.

montanate **1** *the trivial name for* octacosanoate, CH_3–$[CH_2]_{26}$–COO^-, the anion derived from montanic acid (i.e. octacosanoic acid), a saturated straight-chain higher fatty acid. **2** any mixture of free montanic acid and its anion. **3** any salt or ester of montanic acid. Montanate esters of long-chain alcohols occur in montan wax, beeswax, and some other natural waxes.

montanoyl *symbol*: Mon; *the trivial name for* octacosanoyl, CH_3–$[CH_2]_{26}$–CO^-, the acyl group derived from montanic acid (i.e. octacosanoic acid).

Monte Carlo method a way of solving a mathematical problem by sampling methods. The procedure involves the construction of a stochastic model of the mathematical process and the performance of sampling experiments upon it. Such methods have application in molecular graphics aimed at extracting the fundamental principles of macromolecular conformation. [After the resort in Monaco famous for its casino.]

Moore, Stanford (1913–82), US protein chemist; Nobel Laureate in Chemistry (1972) jointly with W. H. Stein 'for their contribution to the understanding of the connection between chemical structure and catalytic activity of the active centre of the ribonuclease molecule' [prize shared with C. B. Anfinsen]; also noted for other work (*see* **Stein**).



monosaccharide structures

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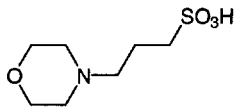
Mops *or* **MOPS** *abbr. for* 3-(*N*-morpholino)propanesulfonic acid; a **Good buffer substance**, pK_a (20 °C) = 7.2.



morgan a unit of genetic length along a chromosome, defined as the distance between two loci that show, on average, one crossover per meiotic event; it is equal to 100 **map units** (or Morgan's units).

Morgan, Thomas Hunt (1866–1945), US geneticist and zoologist noted for developing *Drosphilia* mutants and for gene mapping; Nobel Laureate in Physiology or Medicine (1933) 'for his discoveries concerning the role played by the chromosome in heredity'.

Morgan's unit *an alternative name for* map unit. *Compare* **morgan**.

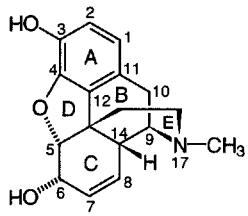
Mörner's test a qualitative test for tyrosine in which a green coloration is produced when a tyrosine-containing sample is boiled in a solution of formaldehyde in strong sulfuric acid. [After K.A.H. Mörner (1855–1917), Swedish chemist.]

morph+ *a variant form of* **morpho+** (before a vowel).

+morph *comb. form* indicating of a specified form, shape, or structure. —**+morphic** *or* **+morphous** *adj.*; **+morphy** *n.*

morphiceptin a tetrapeptide amide fragment of the milk protein β-casein, structure Tyr-Pro-Phe-Pro–NH_2. It relates to the N-terminal tetrapeptide of casomorphin. It is a potent and specific agonist for μ-opiate receptors, its effects on the receptor being blocked by naloxone.

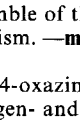
morphine 7,8-didehydro-4,5-epoxy-17-methylmorphinan-3,6-diol; an opiate and the most important opium alkaloid; it is a powerful, habit-forming narcotic analgesic. The diacetate ester, diacetylmorphine, is known as **diamorphine** or **heroin**. This is strongly habit forming and its manufacture, importation, and use are controlled in a number of countries.



morpho+ *or (before a vowel)* **morph+** *comb. form* indicating form or structure.

morphogenesis the ensemble of the processes of development of a part, organ, or organism. —**morphogenetic** *or* **morphogenic** *adj.*

morpholine tetrahydro-1,4-oxazine; a heterocyclic compound with a six-membered oxygen- and nitrogen-containing ring. A number of *N*-substituted morpholines are useful as biological buffers, e.g. **Mes**, **Mops**.



morphology the branch of biology concerned with the outer form and inner structure of living organisms.

Morquio syndrome *another name for* mucopolysaccharidosis IV. *See* **mucopolysaccharidosis**.

mortalin *other name*: 75 kDa glucose regulated protein (*abbr.*: GRP 75); a protein that resembles **heat-shock proteins** in sequence, and which may be a **chaperone**. It is a member of the heat-shock protein 70 family, which functions as a mortality marker in fibroblasts. Mortal fibroblasts contain a protein, MOT-1, uniformly distributed in the cytosol, while in immortal fibroblasts another form of the protein, MOT-2, is concentrated in perinuclear or juxtanuclear regions. In MOT-2 there are differences at residues 618 (Val to Met) and 624 (Arg to Gly). The cytosolic form induces cellular senescence, the perinuclear form does not. Example (precursor), MOT-1 from mouse: database code GR75_MOUSE, 679 amino acids (73.45 kDa).

MOS a gene family encoding serine/threonine kinases, e.g. the human and mouse protein pp39^{mos}; v-*mos* is the oncogene of the acutely transforming murine Moloney sarcoma virus (hence 'mos' from mo + s). *MOS* mRNA is detectable only in germ cells in testes and ovaries, and *MOS* expression is implicated in meiosis; directly or indirectly it stabilizes **M-phase promoting factor** and activates **MAP kinase**. The protein has homology with Src (*see* **src**) but is not a tyrosine kinase. Example from human: database code KMOS_HUMAN, 346 amino acids (37.82 kDa).

mosaic **1** a design or pattern on a surface, made up numerous separate pieces of more or less the same area but differing in some characteristic, e.g. colour, shape, texture. **2** *an alternative name for* **chimera** (used especially of animals).

mosaic model *see* **fluid-mosaic model**.

MOT-1, MOT-2 *see* **mortalin**.

mother liquor the liquid remaining after a substance has been crystallized or precipitated from a solution.

motif (in relation to protein structure) **1** a locally ordered region within the hydrophobic core of a globular protein molecule, formed by three-dimensional interaction between two or three segments of the secondary structure (α helix and/or β strand) that are near one another along the polypeptide chain. The most important types are: (αα), (αβ), (βββ), and (βαβ). *See also* **domain**. **2** *or* **rule** any set of amino acids forming part of the primary sequence of a protein, either contiguous or capable of being aligned to certain positions that are invariant or conserved, that is associated with a particular function; e.g.the motif GXGXXG is associated with nucleotide-binding sites. *See also* **Appendix E**.

motile (of organisms or cells) capable of independent locomotion; (of cilia, flagella, etc.) capable of spontaneous movement. —**motility** *n.*

motilin a 22-residue peptide produced by **Mo cells** of the mucosa of the upper small intestine and having putative hormonal activity. Its plasma level rises when food or alkali is placed in the duodenum and it stimulates contractions of the stomach and the secretion of pepsin, but its effects show marked species variation. Example from dog: database code MOTI_CANFA, sequence

FVPIFTHSELQKIREKERNKGQ

(2.685 kDa).

motor *(in biology)* pertaining to movement of an organ or part; pertaining to nerves or neurons involved in muscular activity.

motor protein a protein, e.g. **dynein**, **kinesin**, **myosin**, that propels itself along a filament or polymeric molecule. Nucleoside triphosphate hydrolysis is usually necessarily involved. A similar process is thought to be involved in the action of elongation factor G (*see* **EF-G**). These processes are referred to as **chemical–mechanical coupling** (or mechanochemical coupling)

Motrin *a proprietary name for* **ibuprofen**.

mould *or (US)* **mold** **1** any **microfungus** having a distinctive mycelium; *the common name for* any superficial growth of fungal mycelium. **2** a matrix for shaping a cast.

moult *or (US)* **molt** **1** to cast off periodically an outer covering of cuticle, feathers, hair, horns, skin, etc. **2** the act, process, or condition of moulting; in invertebrates it is known as ecdysis.

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moulting hormone *or (US)* **molting hormone** *a common name for* **ecdysterone**.

mouse-convulsion method a sensitive method for the detection and biological assay of insulin, used primarily to control the strength of pharmaceutical preparations of insulin. It is based on the finding that small doses of insulin injected into mice (0.1–1.0 μg per animal) cause convulsions. When the method is used for assay, large equal numbers of animals are injected with either of two dilutions of the test solution or of a standard and the results are analysed statistically.

mouse mammary tumour virus *abbr.*: MMTV; a DNA virus that causes breast cancer in mice. The virus contains a powerful enhancer DNA sequence in the terminal repeats of the genome. This activates an oncogene called *wnt-1* (formerly called *int-1*) which is closely homologous to the *Drosophila* gene ***wingless***. MMTV is often used as an **expression vector** especially in transgenic mice.

moving-boundary electrophoresis an analytical method of electrophoresis carried out using a **Tiselius apparatus**, formerly used for measuring electrophoretic mobility directly.

MOX *abbr. for* methanol oxidase (*see* **alcohol oxidase**).

m.p. *abbr. for* melting point.

MP *abbr. for* mitogenic protein (i.e. **interleukin 1**).

6-MP *abbr. for* 6-mercaptopurine.

MPF *abbr. for* M-phase-promoting factor.

M phase the period of mitosis and cytokinesis in the eukaryotic **cell-division cycle**. During this phase the nucleus and cytoplasm divide.

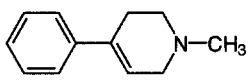
M-phase-promoting factor *or* **maturation-promoting factor** *or* **p34^{cdc}** *abbr.*: MPF; a protein complex, containing **cyclin** and a protein kinase, that triggers a cell to enter M phase of the **cell-division cycle**. Example, protein kinase of meiotic maturation of *Xenopus* oocytes: database code A44349, 302 amino acids (34.47 kDa).

MPP *abbr. for* mitochondrial processing peptidase.

M6P receptor *abbr. for* **mannose 6-phosphate receptor**.

M protein **1** a structural protein that occurs in the M lines of myofibrils of striated muscle. **2** *an alternative name for* galactoside permease of *Escherichia coli*. **3** a cell-surface protein of Gram-positive cocci, associated with virulence; it renders the organism resistant to phagocytosis. It is a cell-wall component, consisting of a coiled coil with membrane anchor. Example from *Streptococcus pyogenes* serotype 6 (precursor): database code M6_STRPY, 483 amino acids (53.41 kDa).

MPTP *abbr. for* 1-methyl-4-phenyl-1,2,3,6-tetrahydropyridine; a toxic by-product of the synthesis of heroin; it produces severe and permanent parkinsonism in primates, resulting from its oxidation by monoamine oxidase to the quaternary 1-methyl-4-phenyl-pyridinium (MPP^+) ion. The latter is a potent inhibitor of complex I of the mitochondrial electron-transport chain and a selective neurotoxin for dopaminergic neurons, by which it is taken up in the substantia nigra via the normal neuronal dopamine re-uptake system.



MRC *abbr. for* Medical Research Council (of the UK).

MRE *abbr. for* metal response element; *see also* **response element**.

MRF *abbr. for* melanotropin-releasing factor (*see* **MSHRH**).

MRF4 *abbr. for* muscle specific regulatory factor 4; *other name*: myogenic factor 6; a DNA-binding, probably **helix-turn-helix** protein of the ***MYC*** family. It induces fibroblasts to differentiate into myoblasts. Example from chicken: database code MYF6_CHICK, 242 amino acids (26.32 kDa).

MRH *abbr. for* melanotropin-releasing hormone (*see* **MSHRH**).

MRI *abbr. for* magnetic resonance imaging.

MRIF *abbr. for* melanotropin release-inhibiting factor (i.e. **melanostatin**).

MRIH *abbr. for* melanotropin-release inhibiting hormone (i.e. **melanostatin**).

mRNA *abbr. for* messenger RNA.

mRNA binding site (ribosome) a ribosomal binding region for mRNA. In bacteria this involves **ribosomal proteins** S1, S3, S4, S5, S12, S18, S21, and the 3′ end of 16S rRNA.

mRNA splicing the process in which excision of **introns** from the primary transcript of **messenger RNA** (mRNA) is followed by ligation of the two **exon** termini exposed by removal of each intron, so that mRNA consisting only of the joined exons is produced. *See* **splicing** (def. 2).

mRNP *abbr. for* messenger ribonucleoprotein

MRSA *abbr. for* **methicillin**-resistant *Staphylococcus aureus*, an organism resistant to antibiotics owing to the inability of penicillins to enter the cell (and not directly to **β-lactamase**). *Compare* **VRE**.

MS *abbr. for* **1** mass spectrometer or mass spectrometry. **2** magic spot (compound). **3** multiple sclerosis.

MS- *abbr. for* meso-.

MSA *abbr. for* multiplication-stimulating activity.

msDNA *abbr. for* multicopy single-strand DNA.

MSEL-neurophysin *see* **neurophysin II**.

MSG *abbr. for* monosodium glutamate.

MSH *abbr. for* melanocyte-stimulating hormone.

MSHIF *abbr. for* melanocyte-stimulating-hormone release-inhibiting factor (i.e. **melanostatin**).

MSHIH *abbr. for* melanocyte-stimulating-hormone release-inhibiting hormone (i.e. **melanostatin**).

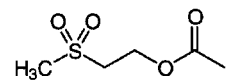
MSHRF *abbr. for* melanocyte-stimulating-hormone releasing factor (i.e. **MSHRH**).

MSHRH *abbr. for* melanocyte-stimulating-hormone releasing hormone; a pentapeptide, possibly identical to the N-terminal moiety of **oxytocin**, that is produced in the hypothalamus. In animals that show an unambiguous response of their melanophores to **melanotropin** this regulating factor is believed to promote melanotropin release. *Recommended name*: melanoliberin; *other names*: melanotropin-releasing factor (*abbr.*: MRF); melanotropin-releasing hormone (*abbr.*: MRH); melanocyte-stimulating-hormone releasing factor (*abbr.*: MSHRF).

MSHRIF *abbr. for* melanocyte-stimulating-hormone release-inhibiting factor (i.e. **melanostatin**).

MSHRIH *abbr. for* melanocyte-stimulating-hormone release-inhibiting hormone (i.e. **melanostatin**).

MSOC *abbr. for* the *N*-(2-methanesulfonyl)ethoxycarbonyl group; it is used as an amino-protecting group, its stability to acid, lability to alkali, and resistance to hydrogenation contributing to its usefulness. It is introduced using such reagents as **methylsulfonyl nitrophenyl carbonate** and **methylsulfonyl succinimidyl carbonate**.



MSX-1 *or* **Hox-7** a **homeobox** protein. Example from human: database code HMX1_HUMAN, 297 amino acids (30.96 kDa).

mtDNA *abbr. for* mitochondrial DNA.

MTOC *abbr. for* microtubule organizing centre.

mtRNA *abbr. for* mitochondrial RNA.

mu *symbol*: μ (lower case) *or* M (upper case); the twelfth letter of the Greek alphabet. For uses *see* **Appendix A**.

MU *abbr. for* 4-methylumbelliferyl.

mu chain *or* **μ chain** the heavy chain characterizing **immunoglobulins** belonging to the class IgM.

mucic acid *an old name for* galactaric acid, the *meso*-aldaric acid derived from both D- and L-galactose.

mucilage any of numerous proteoheteroglycans, frequently containing uronic acids, that occur widely in plants, especially

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in seed coats. Mucilages are hard when dry, and in water they swell, but do not dissolve, to form slimy masses with adhesive properties. *Compare* **gum**. —**mucilaginous** *adj.*

mucin any of a group of widely distributed glycoproteins of high M_r that are secreted by various animal mucous cells and glands; they occur, e.g., in saliva, gastric juice, and intestinal juice. Mucins form viscous solutions that act as lubricants and protectants of the linings of body cavities and of the skin. Example from human intestine: database code HUMMUC2X, 5179 amino acids (539.70 kDa).

mucinase *an alternative name for* **hyaluronidase**.

muco+ *comb. form* of mucus or mucin; mucoid.

mucoid **1** any **mucin**-like substance or mucoprotein. **2** of the nature of or resembling **mucus**. **3** describing a bacterial colony that has a gummy consistency, resulting from the abundant synthesis of capsular material.

mucolipid *an alternative name for* **ganglioside**.

mucolipidosis (*pl.* **mucolipidoses**) any of a group of inherited autosomal recessive diseases of humans characterized by deficiency of a variety of lysosomal hydrolases in connective tissue cells of patients, and in fibroblasts cultured from them. Mucolipidosis I, commonly known as **sialidosis**, is due to a deficiency of neuraminidase that leads to accumulation of sialyl oligosaccharides, and excretion of these in the urine. In mucolipidosis II, the cytoplasm of cultured cells from affected patients contains numerous highly refractile inclusions, visible by phase-contrast microscopy. These are very large lysosomes containing heterogeneous material, mucopolysaccharides, glycolipids, and whorls of membranes, giving this the name **I-cell** (inclusion cell) **disease**. Mucolipidosis III is due to a deficiency of N-acetylglucosamine 1-phosphotransferase.

mucolytic having the ability to disrupt mucus.

muconate *a trivial name for* any one of the three stereoisomers (*cis,cis*, *cis,trans*, or *trans,trans*) of 2,4-hexadienedioate; 1,3-butadiene-1,4-dicarboxylate; $^{-}$OOC–CH=CH–CH=CH–COO^{-}, the dianion derived from muconic acid. The *cis,cis* isomer is an intermediate in the degradation of catechol by microorganisms.

muconolactone Δ-isomerase EC 5.3.3.4; an enzyme that catalyses the reaction:

2,5-dihydro-5-oxofuran-2-acetate = 3,4-dihydro-5-oxofuran-2-acetate

in the pathway for the degradation of catechol to acetyl-CoA. Example from *Pseudomonas putida*: database code NRL_1MLI, 96 amino acids (11.15 kDa); 3-D structure known.

mucopeptide *(sometimes) an alternative name for* **peptidoglycan**.

mucopolysaccharide any of a group of acid heteroglycans built up of characteristic repeating disaccharide units each consisting of an *N*-acylated hexosamine residue and a uronic-acid residue; many mucopolysaccharides also contain sulfate. The group includes hyaluronic acid (*see* **hyaluronate**), **chondroitin sulfate**, **dermatan sulfate**, **keratan sulfate**, **heparin**, and some **blood-group substances**.

mucopolysaccharide storage disease any of a group of clinically progressive, hereditary diseases of humans characterized by the accumulation of mucopolysaccharides in various tissues. They include the **mucopolysaccharidoses** and the **mucolipidoses**.

mucopolysaccharidosis (*pl.* **mucopolysaccharidoses**) any of a group of clinically progressive, hereditary diseases of humans each of which is characterized by the deficiency of a single lysosomal hydrolase concerned in the degradation of mucopolysaccharides. They have been classified into a number of types. *See* individual entries below.

mucopolysaccharidosis I H *or* **Hurler syndrome** a **mucopolysaccharidosis** caused by a deficiency in lysosomal L-iduronidase (EC 3.2.1.76) that affects the degradation of both dermatan sulfate and heparan sulfate. It is inherited as an autosomal recessive disorder. Subjects excrete excessive amounts of both dermatan sulfate and heparan sulfate in the urine in the ratio of approximately 7:3. The biochemical lesion is the same as in mucopolysaccharidoses I H/S and I S, from which differentiation can only be made by clinical criteria.

mucopolysaccharidosis I H/S *or* **Hurler–Scheie compound syndrome** a **mucopolysaccharidosis** caused by the same deficiency in lysosomal L-iduronidase (EC 3.2.1.76) as is found in mucopolysaccharidoses I H and I S. It is inherited as an autosomal recessive disorder and it is believed to be a phenotype intermediate between these two syndromes, one mutant allele being inherited from the father and a different mutant allele from the mother. The condition can only be differentiated from mucopolysaccharidoses I H and I S by clinical criteria.

mucopolysaccharidosis I S *or* **Scheie syndrome** *or (formerly)* **mucopolysaccharidosis V** a **mucopolysaccharidosis** caused by the same deficiency in lysosomal L-iduronidase (EC 3.2.1.76) as is found in mucopolysaccharidoses I H and I H/S. It is inherited as an autosomal recessive disorder and it has a milder clinical course than mucopolysaccharidoses I H and I H/S, from which it can be differentiated only by clinical criteria.

mucopolysaccharidosis II *or* **Hunter syndrome** a **mucopolysaccharidosis** caused by a deficiency in iduronate sulfatase that affects the degradation of both dermatan sulfate and heparan sulfate. It is inherited as an X-linked recessive disorder, and several different mutations of the same X-chromosome locus probably account for the different severities of the disease seen in various families. Subjects excrete excessive and roughly equal amounts of both dermatan sulfate and heparan sulfate in the urine.

mucopolysaccharidosis III A *or* **Sanfilippo syndrome A** a **mucopolysaccharidosis** caused by a deficiency in heparan *N*-sulfatase that affects the degradation of heparan sulfate. It is inherited as an autosomal recessive disorder and is indistinguishable clinically from mucopolysaccharidosis III B. Subjects excrete excessive amounts of heparan sulfate in the urine.

mucopolysaccharidosis III B *or* **Sanfilippo syndrome B** a **mucopolysaccharidosis** caused by deficiency in α-*N*-acetyl-D-glucosaminidase (EC 3.2.1.50) that affects the degradation of heparan sulfate. It is inherited as an autosomal recessive disorder and is indistinguishable clinically from mucopolysaccharidosis III A. Subjects excrete excessive amounts of heparan sulfate in the urine.

mucopolysaccharidosis IV A (*or* **IVa**) *or* **Morquio A disease** a mucopolysaccharidosis caused by a deficiency of lysosomal *N*-acetylgalactosamine-6-sulfatase, leading to an accumulation of keratan sulfate and chondroitin 6-sulfate. It is inherited as an autosomal recessive disorder.

mucopolysaccharidosis IV B (*or* **IVb**) *or* **Morquio B disease** a mucopolysaccharidosis caused by a deficiency of β-galactosidase leading to accumulation of keratan sulfate. It is inherited as an autosomal recessive disorder.

mucopolysaccharidosis V *a former name for* **mucopolysaccharidosis I S**.

mucopolysaccharidosis VI *or* **Maroteaux–Lamy syndrome** a **mucopolysaccharidosis** caused by a deficiency of lysosomal *N*-acetylgalactosamine 4-sulfatase that affects the degradation of dermatan sulfate. Three clinically distinguishable forms are known: severe, intermediate, and mild; all are inherited as autosomal recessive disorders, with probably two or more mutant alleles at the mucopolysaccharidosis VI locus, one of which produces the severe form when homozygous and the other the mild form. Subjects excrete excessive amounts of dermatan sulfate in the urine.

mucopolysaccharidosis VII a **mucopolysaccharidosis** caused by a deficiency of lysosomal β-D-glucuronidase (EC 3.2.1.31) that affects the degradation of both dermatan sulfate and heparan sulfate. It is inherited as an autosomal recessive disorder.

mucoprotein any glycoprotein containing relatively large amounts of acidic polysaccharide.

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mucosa (*pl.* **mucosae**) *or* **mucous membrane** any of the moist membranes that line the alimentary canal, the glandular ducts, and the respiratory, urinary, and genital passages; it may be smooth, corrugated, or covered with villi. Mucous membranes consist of a surface layer of epithelium containing mucus-secreting glands, and an underlying layer of connective and muscular tissue. *Compare* **serosa**. —**mucosal** *adj.*

mucotetraose *symbol*: $McOse_4$ *or* Mc_4 (if space is limited); the tetrasaccharide Gal(β1-3)Gal(β1-4)Gal(β1-4)Glc.

mucotriaose *symbol*: $McOse_3$ *or* Mc_3 (if space is limited); the trisaccharide Gal(β1-4)Gal(β1-4)Glc.

mucous relating to, resembling, or secreting **mucus**.

mucous cell any cell that secretes **mucus**.

mucous gland any exocrine gland consisting predominantly of **mucus**-secreting cells.

mucous membrane *an alternative name for* **mucosa**. *Compare* **serous membrane**. —**mucomembranous** *adj.*

mucus the slimy, sticky, viscous secretion, consisting predominantly of **mucins**, that is secreted by mucous cells of the mucosae and of the external body surface of some animals.

MUG *abbr. for* **1** either 4-methylumbelliferyl-glucuronide or 4-methylumbelliferyl-β-D-galactopyranoside. Both compounds are fluorogenic enzyme substrates that yield 4-methylumbelliferone. *See also* 4-**methylumbelliferyl**. **2** *abbr. for* murinoglobulin.

MUGal *abbr. for* 4-methylumbelliferyl-β-D-galactopyranoside (alternative to MUG).

mull a suspension of very finely ground solid in an inert liquid, especially paraffin or **Nujol**, that is used in infrared spectroscopy of the solid.

Muller, Hermann Joseph (1890–1967), US geneticist; Nobel Laureate in Physiology or Medicine (1946) 'for the discovery of the production of mutations by means of X-ray irradiation'.

Mullis, Kary B. (1944–), US biochemist; Nobel Laureate in Chemistry (1993) 'for his invention of the polymerase chain reaction (PCR) method' [prize (awarded 'for contributions to the developments of methods within DNA-based chemistry') shared with M. Smith].

multi+ *comb. form* denoting more than one, several. *See also* **poly+**.

multicatalytic endopeptidase complex *see* **proteosome**.

multicellular having, or consisting of, several or many cells.

multichain (of a protein) consisting of two or more polypeptide chains connected by nonpeptide links.

multichannel analyser any instrument or device for sorting a heterogeneous input into a number of ranges, e.g. of frequency or energy, and determining the relative proportions in each range.

multicopy single-strand DNA *abbr.*: msDNA; DNA generated by bacterial reverse transcriptase and found in certain Gram-negative bacteria. The molecules are unique in being the only known naturally occurring examples of nucleic acids containing an RNA–DNA covalent link.

multidentate (of a ligand) having two or more groups through which it can be attached to a central atom. Such a ligand is able to form a bridge or a chelate.

multidimensional chromatography a technique in which a single component separated from a mixture by chromatography on one type of column may be automatically transferred, as a sample, for chromatography on another type of column in order to effect further resolution.

multienzyme *the recommended class name for* any protein that possesses two or more autonomous catalytic functions due to separate catalytic domains (*see* **domain**, def. 3), whether contributed by distinct subunits (*see* **multienzyme complex**), by distinct parts or an individual polypeptide chain (*see* **multienzyme polypeptide**), or by both. Excluded is any enzyme that can catalyse different reactions at the same catalytic centre. *Compare* **enzyme complex**, **multienzyme system**.

multienzyme cluster *see* **enzyme cluster**.

multienzyme complex *the recommended subclass name for* any multienzyme in which catalytic domains occur on more than one type of polypeptide chain. A multienzyme complex may itself contain a **multienzyme polypeptide**.

multienzyme polypeptide *the recommended subclass name for* any multienzyme in which at least two demonstrably distinct catalytic domains of different types occur on a single polypeptide chain and are encoded by a single gene. A multienzyme polypeptide may itself be a component of a multienzyme complex. *Compare* **multifunctional protein**.

multienzyme system *an operational term for* any system of two or more enzymes functioning sequentially to catalyse the reactions of a metabolic pathway, so that the product of the first enzyme becomes the substrate of the second and so on. Three levels of organization of multienzyme systems may be discerned. First, the individual enzymes are independently in solution in the cytoplasm and are not directly associated with each other when acting. Second, the individual enzymes are physically associated and function together as an **enzyme complex**, or they occur as a **multienzyme**. Third and most highly organized, the individual enzymes are associated with large, supramolecular structures such as membranes or ribosomes. *See also* **enzyme cluster**, **metabolon**.

multidrug resistance *see* **MDR**.

multifactorial **1** involving or dependent on more than one factor or causes. **2** *(in genetics)* inheritance depending on more than one gene.

multifunctional protein any protein that combines two or more autonomous functions on one polypeptide chain, the functions being both independently measurable and assignable to separate domains of the protein. Such functions may or may not be catalytic (*compare* **multifunctional protein ade2**). Excluded are allosteric enzymes, proenzymes, and enzymes that can catalyse different reactions at a single reaction centre.

multifunctional protein ade2 a protein that contains **phosphoribosylaminoimidazolesuccinocarboxamide synthase** and **phosphoribosylaminoimidazole carboxylase** and is involved in the sixth and seventh steps in *de novo* purine biosynthesis. Example from human: database code PUR6_HUMAN, 425 amino acids (47.03 kDa); the synthase domain resides in residues 1–260, the carboxylase domain in residues 261–425.

multigenic describing character differences that are controlled by the alleles of several genes.

multiiodinated describing any compound that has been reacted so as to contain two or more atoms of iodine per molecule.

multilamellar occurring as, or made up of, several discrete layers.

multilayered film analyser a device for the rapid determination of any of a range of components present in small volumes of biological fluids. It depends on a single-use reagent slide on which the various chemicals required are present in dry form as a series of thin films. These consist successively of an indicator layer, a semipermeable layer, a reagent layer, and a spreading layer, all mounted between two transparent supports. Typically, a 10 µL sample is applied to the spreading layer, a chemical or enzymatic reaction occurs in the reagent layer, and the semipermeable layer withholds macromolecular substances from the indicator layer, where usually a dye combines with a product of the reaction to form a coloured compound. The intensity of the colour, which is proportional to the quantity of the analyte in the specimen, is measured by reflectance spectrophotometry. The concept has been extended to the use of potentiometry for the measurement of sodium and potassium.

multilocus enzyme any of a set of enzymes, with similar catalytic properties and existing in the same organism, whose amino-acid sequences are encoded in nonallelic structural genes at two or more separate loci. There may be marked variations in the expression of the individual loci in different tissues. A class of **isoenzyme**.

multimer any specific aggregate of (identical or nonidentical) molecular entities held together by noncovalent bonds.

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—**multimeric** *adj.*; **multimerize** *or* **multimerise** *vb.*; **multimerization** *or* **multimerisation** *n.*

multinucleate *or* **multinuclear** (of a cell) containing several or many nuclei.

multiphase having several phases; polyphase.

multiple codon recognition the recognition by a single tRNA molecule of more than one type of codon in mRNA.

multiple development technique a chromatographic technique in which the chromatogram is developed more than once with either the same solvent system or a different one with the aim of improving the separation.

multiple drug resistance *see* **MDR**.

multiple forms (of an enzyme) *the recommended collective term to describe* all proteins that possess the same (specified) enzymic activity and occur naturally in a single species. It includes, but is not limited to, **isoenzymes**; the term isoenzyme should be applied only to multiple forms that arise from genetically determined differences in primary structure, and some limit this to those arising from a single gene locus.

multiple myeloma *or* **multiple myelomatosis** *see* **myeloma**.

multiple sclerosis *abbr.*: MS; a chronic and usually progressive disease of the nervous system, also known as disseminated sclerosis, in which the myelin sheaths surrounding the axons are lost; the lesions are confined to the central nervous system. The cause is unknown, but plaques are found in which activated lymphocytes and monocytes are present; these plaques have a discrete edge and range in size from microscopic to macroscopic. The disease is characterized by a course of relapses and remissions over a number of years.

multiplet any group of two or more associated spectral lines. In electronic spectra the lines of a multiplet are very closely spaced and appear at low resolution as a single line, whereas in nuclear magnetic resonance spectra the separation may be considerable.

multiplicand *(in mathematics)* a number to be multiplied by another number – the multiplier – in an arithmetic multiplication.

multiplication-stimulating activity *abbr.*: MSA; an activity found in mammalian serum and produced by some animal cells that is required for the multiplication of animal cells in culture.

multiplicity *(in physics)* the number of components in a **multiplet**.

multiplicity of infection the ratio of the number of virus particles to the number of susceptible cells in a given system.

multiplicity reactivation the reconstruction of viable genomes in a cell that is multiply infected with otherwise nonviable viruses.

multiplier **1** *(in mathematics)* any number by which another number – the multiplicand – is multiplied. **2** any instrument or device for multiplying an effect, e.g. photomultiplier.

multiply labelled describing an isotopically substituted compound that has more than one modified atom of the same element at the same position or at different positions.

multipotent (of a cell or tissue) capable of giving rise to several kinds of cells, tissues, or structures. *Compare* **pluripotent** (def. 2).

multisubstrate enzyme any enzyme that requires two or more substrates in order to catalyse a particular reaction.

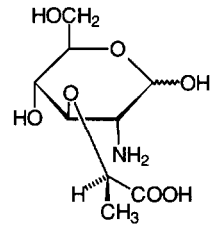
multivalent *an alternative term for* **polyvalent**.

multivalent phosphorylation the phosphorylation of any hormonally regulated enzyme at a plurality of sites by two or more distinct kinase enzymes, with a resultant increase in the regulatory potential of the enzyme.

multivesicular body an intracellular structure that is lined by a single membrane and contains a number of inner vesicles that are approximately 50 nm in diameter. It is a form of secondary **lysosome**.

Mur *symbol for* a residue (or sometimes a molecule) of **muramic acid**.

muramic acid *symbol*: Mur; 3-*O*-α-carboxyethyl-D-glucosamine; the 3-*O*-D-lactyl ether derivative of D-glucosamine. It occurs naturally in peptidoglycan of bacterial cell walls.



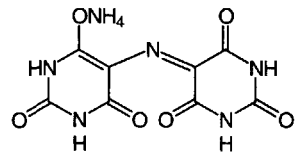
muramidase *an alternative name for* **lysozyme**.

muramyl the acyl group derived from **muramic acid**.

muramyl-dipeptide *abbr.*: MDP; *N*-acetyl-muramyl-D-alanyl-D-isoglutamine; a synthetic, water-soluble, **peptidoglycan** derivative that is capable of replacing whole mycobacteria in complete **Freund's adjuvant**. It is highly active in stimulating antibody production against an antigen injected simultaneously.

murein *an alternative name for* **peptidoglycan**.

murexide ammonium purpurate; 5,5′-nitrilodibarbituric acid monoammonium salt; a compound that forms a purple-red solution in water. It is useful as an indicator in complexometric titration of calcium, nickel, cobalt, copper, etc. with EDTA.



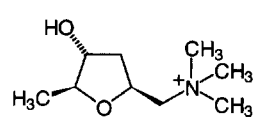
murexide test a colour test for uric acid and some other purines. The (solid) sample is first treated with conc. nitric acid, which is slowly evaporated away; subsequent addition of ammonia solution gives a purple colour if uric acid was present, due to formation of murexide, or a yellow colour that turns to red on heating if xanthine was present.

murine of, belonging to, characteristic of, affecting, transmitted by, or being a member of the Muridae, a family of small rodents that includes mice and rats; of or relating to the mouse genus, *Mus*.

murinoglobulin *abbr.*: MUG; a monomeric proteinase inhibitor found in blood plasma of vertebrates and invertebrates and in egg white of birds and reptiles. It has a characteristic **bait region**. Example, murinoglobulin 2 (MUG2) precursor from mouse: database code A2MH_MOUSE, 1451 amino acids (162.18 kDa). *Compare* α_2 **macroglobulin**.

muropeptide *an alternative name for* **peptidoglycan**.

muscarine a toxic alkaloid (quaternary ammonium base) found in the red variety of *Amanita muscaria* (fly agaric) and some other gill fungi. It is an agonist for one type of **cholinoceptor**.



(+)-enantiomer

muscarinic receptor *see* **cholinoceptor**.

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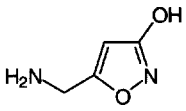
muscimol 5-aminomethyl-3-hydroxyisoxazole; an isoxazole isolated from the fungus *Amanita muscaria*. A hallucinogen and potent CNS depressant, it is a selective agonist of $GABA_A$ receptors.



muscle 1 a tissue made up of various elongated cells that are specialized to contract and thus to produce movement and mechanical work. 2 an organ consisting principally of muscle tissue. *See* **cardiac muscle**, **smooth muscle**, **striated muscle**. —**muscular** *adj.*

muscle contraction *see* **sliding filament model**.

muscle hemoglobin *a former name for* **myoglobin**.

muscle sugar *a former name for* **inositol** (def. 1).

muscular dystrophy any of a number of genetically determined diseases of humans in which there is progressive muscular weakness and evidence of muscle degeneration. All are characterized by creatinuria, and serum creatine phosphokinase activity is elevated in several of them. *See also* **dystrophin**.

mushroom sugar *a former name for* **trehalose**.

mustard gas sulfur mustard; bis(2-chloroethyl)sulfide; a colourless oily liquid with a very low vapour pressure. It is a powerful vesicant and also a mutagen and carcinogen. *See also* **nitrogen mustard**.

mustard oil any alkyl isothiocyanate, of general formula R–N=C=S. Such compounds have a pungent mustard-like smell and are present in the tissues of a number of plants, either free or as thioglycosides.

mut any of a family of genes whose products are involved in **mismatch repair**. All the following examples are from *Escherichia coli*. The product of *mutH* is a repair endonuclease that is specific for unmethylated GATC sequences: database code MUTH_ECOLI, 228 amino acids (25.36 kDa). The protein encoded by *mutL* is also involved in repair of mismatches in DNA and is required for activity of the *dam* product; database code MUTL_ECOLI, 615 amino acids (67.85 kDa). The protein encoded by *mutS*, again involved in mismatch repair (possibly the recognition step), has weak ATPase activity; database code MUTS_ECOLI, 853 amino acids (95.14 kDa).

mutable able or tending to undergo change or **mutation**. —**mutability** *n.*

mutable gene any gene that spontaneously mutates at a high rate.

mutable site any site on a chromosome at which mutations can occur.

mutagen any physical or chemical agent that is capable of increasing the frequency of **mutation** above the spontaneous, background level. —**mutagenic** *adj.*; **mutagenicity** *n.*

mutagenesis the production of mutations.

mutagenize *or* **mutagenise** to treat (cells or organisms) with a mutagen. —**mutagenized** *or* **mutagenised** *adj.*

mutant 1 **a** any organism that has arisen by or has undergone **mutation**, or one that carries a mutant gene that is expressed in the phenotype of that organism. **b** a mutant gene. 2 produced by or following a mutation; having the attributes of a **mutant** (def. 1).

mutarotation the spontaneous change in the optical rotation of a freshly prepared solution of a pure stereoisomer, especially a carbohydrate, that is caused by epimerization, or some other structural change.

mutase any enzyme that catalyses (or apparently catalyses) an intramolecular transfer of a chemical group. Such enzymes belong to one of the following EC sub-subclasses: EC 5.4.1, transferring acyl groups; EC 5.4.2, transferring phosphoryl groups; EC 5.4.3, transferring amino groups; EC 5.4.99, transferring other groups.

mutate to undergo or cause to undergo mutation.

mutation 1 the process by which genetic material undergoes a detectable and heritable structural change, or the result of such a change. Three categories are recognized: **genome mutations**, in which addition or subtraction of one or more whole chromosomes occurs; **chromosome mutations**, in which the structure of one or more chromosomes is affected; and **gene mutations**, in which the structure of a gene is altered at the molecular level. 2 any modified gene arising from a **mutation** (def. 1). 3 a **mutant** (def. 1). *See also* **deletion**, **inversion** (def. 4), **point mutation**, **translocation** (def. 2).

mutational heteroduplex *see* **heteroduplex**.

mutation frequency the frequency at which a mutation occurs in a population. It may or may not reflect the **mutation rate**, with which it is sometimes used interchangeably.

mutation frequency decline the significant and irreversible reduction in the frequency of some UV-induced mutations in bacteria during the temporary post-irradiation inhibition of protein synthesis.

mutation pressure the continued production of an allele by mutation that tends to increase the allele's frequency in the gene pool.

mutation rate 1 the probability that a particular mutation will occur per virus, cell, or organism during a reproductive cycle. 2 the frequency at which any mutation or mutational class occurs in a given population; **mutation frequency**.

mutator gene any gene that produces an increase in spontaneous mutation rates. Their action may be limited to certain alleles or to certain mutational pathways.

mutein a mutant protein produced by site-specific mutagenesis or other recombinant DNA technique.

muton the smallest unit of genetic material whose alteration may give rise to a mutation; commonly supposed to be a single nucleotide (pair).

MVA *abbr. for* mevalonic acid (use discouraged).

MVG *abbr. for* methoxyvinylglycine.

M.W. *abbr. for* molecular weight (alternative to mol. wt.).

MWC model *abbr. for* Monod–Wyman–Changeux model.

my+ *a variant form of* **myo+** (before a vowel).

MYB a gene family that encodes DNA-binding proteins; v-*myb* is the oncogene of the acutely transforming avian myeloblastosis virus. It is highly conserved between mammalian species. The product, Myb, contains DNA-binding, transcriptional activation, and negative regulatory domains; it recognizes YAAC(G/T)G. It is notably associated with cells of the hemapoietic lineage and is essential for normal hemopoiesis. Example from human: database code MYB_HUMAN, 640 amino acids (72.38 kDa). [From 'myeloblastosis'.]

MYC a family of genes encoding short-lived nuclear regulatory proteins that act as transcription factors, e.g. pp64/pp67 (based on expressed mass). The oncogene, v-*myc*, was originally identified in avian myelocytomatosis virus, MC29, but is also carried by the avian retroviruses CM11 and OK-10. The protooncogene, c-*myc*, is a member of a family of at least seven related genes: *myc*, B-*myc*, N-*myc*, L-*myc*, P-*myc*, R-*myc*, S-*myc*; B-Myc lacks the basic helix-loop-helix leucine zipper (bHLHLZ) domains of other Myc proteins. The product of c-*myc* binds nonselectively to DNA and (with higher affinity) to CAC[GA]TG. In normal cells *myc* expression is strictly dependent on mitogenic stimuli and is required for cell proliferation as well as to prevent cell differentiation. Induction of c-*myc* in the absence of growth factors is sufficient to drive rodent fibroblasts into the cell cycle but concomitantly induces apoptosis unless specific survival cytokines are present. Structurally, the product Myc contains an N-terminal transactivation domain that activates transcription of the gene with which it interacts, and a C-terminal bHLHLZ motif, which is known to mediate Myc dimerization and sequence-specific DNA binding. Although Myc–Myc dimers can form in solution, Myc homodimers are not detected *in vivo*, dimers forming with other partners, e.g. Max, which has a bHLHLZ

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motif but no transactivation domain (*see* ***MAX***). *In vitro*, Myc–Max (and Myc–Myc) dimers have been found to bind DNA with a core sequence of CACGTG. Unlike Myc, Max is a stable protein expressed constitutively in growing, resting, and differentiating cells, and is capable of binding further proteins, e.g. Mad and Mxii, which compete with Myc for binding. The *myc* gene may be activated to become a transforming gene by proviral insertion, chromosomal translocation, or gene amplification, but generally protein structure is not affected; **Philadelphia chromosome** is one example. The *myc* gene has been implicated in various neoplasms in birds, mice, and humans, oncogenic activation occurring mainly through constitutive and elevated expression of the Myc protein. Example from human (six motifs): database code MYC_HUMAN, 439 amino acids (48.75 kDa). [From 'myelocytomatosis'.]

myc+ *a variant form of* **myco+** (before a vowel).

mycarose 2,6-dideoxy-3-*C*-methyl-L-*ribo*-hexose; a component of several **macrolide** antibiotics.

mycelia the plural of **mycelium**.

mycelium (*pl.* **mycelia**) the network or mass of discrete hyphae that forms the body (thallus) of a fungus. —**mycelial** *adj.*

myceto+ *or (before a vowel)* **mycet+** *comb. form* denoting fungus.

myco+ *or (before a vowel)* **myc+** *comb. form* denoting fungus.

mycobacterium (*pl.* **mycobacteria**) any bacterium belonging to the genus ***Mycobacterium***.

Mycobacterium a genus of Gram-positive, aerobic, non-motile, non-spore-forming, acid-fast bacteria of the family Mycobacteriaceae. The cells are rodlike and can form filaments or branched structures; their cell walls characteristically contain **mycolic acid**. Some species are pathogenic to humans and/or other animals, e.g. *M. tuberculosis* (the tubercle bacillus) and *M. leprae* (the leprosy bacillus).

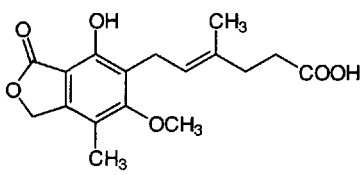
mycobactin any of a family of **siderochromes** of the hydroxamic acid-derivative category, produced by various species of *Mycobacterium*. At least nine have been characterized.

mycolic acid any of a family of α-substituted β-hydroxylated very-long-chain fatty acids of general formula R_2–CH(OH)–CHR_1–COOH, where R_1 is a C_{20}–C_{24} linear alkyl group and R_2 is a complex C_{30}–C_{60} group of very variable structure. They occur naturally as esters of arabinose in the cell walls of *Mycobacterium* spp., *Nocardia* spp., and *Corynebacterium* spp. and as esters of trehalose in **cord factor**. *See also* **cyclic fatty acids**.

mycology the scientific study of fungi. —**mycological** *or* **mycologic** *adj.*; **mycologist** *n.*

mycolyl *the generic name for* acyl groups derived from **mycolic acids**.

mycophenolic acid 6-(1,3-dihydro-4-hydroxy-6-methoxy-7-methyl-3-oxo-5-isobenzofuranyl)-4-methyl-4-hexenoic acid; an antibiotic and antitumour material from *Penicillium brevicompactum*. It was first isolated in 1896, and said by **Florey** to be 'the first antibiotic produced by a mould to be crystallized'. As the morpholinoethyl ester (mycophenolate mofetil) it is an approved immunosuppressant in renal transplantation.

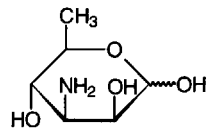


mycoplasma *or (formerly)* **pleuropneumonia-like organism** (*abbr.*: PPLO) any member of the Mycoplasmatales, an order of minute, Gram-negative, prokaryotic microorganisms that are the smallest known free-living organisms. They have no cell walls (except for some saprophytic species), are variable in form, and can pass through bacteria-retaining filters. Some are saprophytic while others are pathogenic to humans, other animals, and plants. Mycoplasmas frequently infect tissue cultures. They were once thought to be the same as **L forms**. A newer classification replaces mycoplasma as a trivial name for members of the entire class by the term **mollicute**, and the class is called Mollicutes. The trivial name 'mycoplasma' is then restricted to members of the genus *Mycoplasma*.

Mycoplasma the main genus of **mycoplasmas**.

mycoprotein a commercially produced protein-containing foodstuff derived from moulds grown on carbohydrate substrates.

mycosamine 3-amino-3-deoxy-D-rhamnose; 3,6-dideoxy-3-amino-D-mannose; an amino sugar that contributes the nitrogen-containing moiety of the polyene antibiotics **amphotericin B** and **nystatin**.



mycose *a common name for* **trehalose**.

mycostatic describing any agent that inhibits the growth of fungi; fungistatic.

mycotoxin any poisonous substance produced by a fungus.

myel+ *a variant form of* **myelo+** (before a vowel).

myelin the material that constitutes the **myelin sheaths** surrounding vertebrate nerve axons. It is rich in lipid, particularly in glycolipid. *See also* **myelin protein**.

myelination the process by which a nerve axon acquires a **myelin sheath**.

myelin protein any of the proteins that form part of the **myelin sheath**. In the following descriptions, all examples are of human precursor sequences. **Myelin-associated glycoprotein**, a cell adhesion molecule for postnatal neural development, is a member of the immunoglobulin superfamily. It is an integral membrane protein. Database code MAG_HUMAN, 626 amino acids (68.99 kDa). **Myelin basic protein**, a protein of the cytoplasmic face of the myelin membrane, is a major protein component of normal myelin of the central nervous system. Very basic in nature (pI > 10.5), it is a single-chain protein of known sequence (human and bovine) and having little tertiary structure. Administration of myelin basic protein in complete **Freund's adjuvant** in various experimental animals elicits experimental allergic encephalitis due to induction of delayed hypersensitivity to the protein, which is suspected of having an important role in the causation of demyelinating diseases in humans. Three forms are produced by alternative splicing. Database code MBP_HUMAN, 196 amino acids (21 arginines, 14 lysines) (21.34 kDa). **P2** is probably a lipid transport protein; it is found in Schwann cells, associated with myelin basic protein. Database code MYP2_HUMAN, 131 amino acids (14.76 kDa). **P0** is an immunoglobulin-like membrane protein of Schwann cells of the peripheral nervous system. It is associated with a hereditary polyneuropathy (Charcot–Marie–Tooth disease type 1b). Database code MYP2_HUMAN, 131 amino acids (14.76 kDa). **Myelin proteolipid protein** (PLP *or* **lipophilin**) is the major myelin protein from the central nervous system, playing an important role in the formation or maintenance of the multilamellar structure of myelin. It is an integral membrane protein. Alternative splicing leads to a shorter variant. Database code MYPR_HUMAN, 276 amino acids (29.91 kDa); identical in mouse, rat, and human. Mutations are associated with Pelizaeus–Merzbacher disease, and other mutations result in dysmyelination, e.g. *jimpy* and *rumpshaker* (mouse) and MD (rat). *See also* **Folch-Lees protein**, **Wolfgram proteolipid protein**.

myelin-proteolipid *O*-palmitoyltransferase EC 2.3.1.100; *other names*: myelin PLP acyltransferase; acyl-protein synthase; an enzyme that catalyses a reaction between palmitoyl-

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CoA and [myelin proteolipid] to form [myelin proteolipid] *O*-palmitoylprotein and CoA.

myelin sheath the sheath that surrounds the axons of vertebrate nerves. It is formed by Schwann cells in peripheral nerves and by oligodendrocytes in the central nervous system; these cells wrap up to 100 concentric layers of their plasma membrane in a tight spiral around the axons. Myelin sheaths prevent almost all electric current leakage across the covered portion of the axon membrane, thereby contributing to the rapid transmission of nerve impulses along the axons. *See also* **myelin**, **myelin protein**.

myelo+ *or (before a vowel)* **myel+** *comb. form* **1** denoting bone marrow. **2** denoting the spinal cord. **3** denoting **myelin**.

myeloblast a cell of the bone marrow that is the precursor of the **myelocyte**.

myelocyte a nucleated cell of the bone marrow that is a precursor of the **granulocytes** of the blood.

myeloid **1** of or pertaining to bone marrow. **2** of or pertaining to the spinal cord. **3** of or resembling myelocytes.

myeloma *or* **myelomatosis** a tumour caused by the uncontrolled proliferation of a clone of immunoglobulin-producing plasma cells. It leads to multiple deposits of tumour cells in the bone marrow and an excessive production of a single type of (i.e. monoclonal) immunoglobulin molecule, which may belong to any of the major classes of immunoglobulins. In some cases either the light or the heavy chains may be produced in excess or exclusively. *See also* **Bence-Jones protein**, **Waldenström's macroglobulinemia**.

myeloma protein an immunoglobulin that is overproduced by a **myeloma**. They are single immunoglobulin types and form the basis of monoclonal antibody technology. Human examples include **Bence-Jones protein**. *See also* **hybridoma**.

myeloperoxidase *a special name for* **peroxidase** (def. 2) from polymorphonuclear leukocytes, so named following its isolation from the blood of patients with myeloid leukemia. It is concerned in the bactericidal action of these cells. It was originally named **verdoperoxidase** on account of its green colour.

Mylar *the proprietary name for* a type of polyethylene terephthalate polyester that forms very strong films of good transparency and high electrical resistance.

myo+ *or (before a vowel)* **my+** *comb. form* denoting muscle.

myo- *prefix* used to distinguish common **inositol**, 1,2,3,5/4,6-cyclohexanehexol (*formerly* ***meso*-inositol**) from the other eight possible inositol stereoisomers.

myoblast any of the mononucleate precursor cells that fuse to form a multinucleate skeletal muscle cell.

myocardium the middle, muscular, layer of the heart wall. —**myocardial** *adj.*

myocyte **1** a muscle cell of any type. **2** any contractile cell.

myoD the gene for myoblast determination protein, it is related to ***MYC***; the human equivalent is *MYF3*. Its product has similar activity to **MRF4**. Example from mouse: database code MYOD_MOUSE, 318 amino acids (34.18 kDa).

myofibre *or (esp. US)* **myofiber** a skeletal muscle fibre; it consists of a single, long, multinucleate cell, composed predominantly of a large number of myofibrils (typically 1000 or more).

myofibril any of the long, cylindrical, contractile elements, 1–2 μm in diameter, that comprise the major component of the cytoplasm of the **myofibre** and extend for its entire length. Each myofibril is composed in turn of numerous **myofilaments**. —**microfibrillar** *adj.*

myofilament either of two kinds of thin, contractile, thread-like, interdigitating structures within the myofibrils of **striated muscle**. The so-called thick filaments are about 15 nm in diameter and 1.6 μm in length, and the so-called thin filaments are about 8 nm in diameter and 1.0 μm in length.

myogen *a name sometimes used for* a number of different protein mixtures extractable with water from skeletal muscle of various species of animal. **Myogen A** is a crystallizable complex of **aldolase** and **glycerol-3-phosphate dehydrogenase** that can be prepared from rabbit muscle.

myogenic factor any of various proteins involved in muscle differentiation. They are normally produced only in muscle cells, but have been shown to activate muscle differentiation mechanisms when introduced into other cells. They include MyoD (*see* ***myoD***), Myf5, and **myogenin**. Example from human: database code MYF4_HUMAN, 224 amino acids (25.01 kDa).

myogenin a protein involved in muscle differentiation (i.e. a **myogenic factor**) that induces fibroblasts to differentiate into myoblasts. It is probably a sequence-specific DNA-binding protein, similar to other members of the Myc family of **helix-turn-helix** transcription factors (*see* ***MYC***). Example from rat: database code MYOG_RAT, 287 amino acids (32.47 kDa).

myoglobin *or (formerly)* **muscle hemoglobin** *or* **myohemoglobin** *abbr.*: Mb; a 17.5 kDa oxygen-carrying hemoprotein that occurs in muscle, particularly in red fibres, and consists of a single polypeptide chain of 153 amino-acid residues to which a single ferroheme prosthetic group is noncovalently bound. Myoglobin binds dioxygen noncooperatively with an affinity between that of hemoglobin and that of cytochrome oxidase. It thus can accept dioxygen from hemoglobin and store it in the muscle cell for release to cytochrome oxidase when the supply becomes limiting. It also assists the direct transfer of dioxygen from the surface of the myocyte to the mitochondria. Sperm-whale myoglobin was the first protein whose three-dimensional stucture was determined by X-ray crystallography. Example from *Sus scrofa domestica* (domestic pig): database code NRL_1PMBA, 153 amino acids (16.93 kDa); 3-D structure known.

myoglobinuria the excretion of myoglobin in the urine.

myohaematin *a historical term*, used by MacMunn for the 'histohaematin' (i.e. the cytochromes) of striated muscle.

myo*-inositol** *an alternative name for* **inositol** (def. 1) (*formerly known as* **muscle sugar**). *See also* ***myo-.

1D-*myo*-inositol-trisphosphate 3-kinase EC 2.7.1.127; an enzyme that catalyses a reaction between ATP and 1D-*myo*-inositol 1,4,5-trisphosphate to form 1D-*myo*-inositol 1,3,4,5-tetrakisphosphate with release of ADP. The enzyme requires calcium. Examples of two human isoforms: database code IP3K_HUMAN, 461 amino acids (50.95 kDa); database code IP3L_HUMAN, 472 amino acids (53.41 kDa). *See also* **inositol phosphates**.

myokinase *an alternative name for* **adenylate kinase**.

myosin any of a group of related proteins with ATPase activity that occur in the contractile apparatus of both muscle and nonmuscle cells; the myosin of striated muscle is the major component of the thick filaments. Individual myosin molecules consist of two identical **heavy chains** of ≈200 kDa and two pairs of light chains (*see* **light chain** (def. 2)) with distinct masses that vary within the range 15–27 kDa according to the source. The N-terminal region of each heavy chain consists of a globular head with which the light chains are associated, and the remaining three-quarters of each heavy chain consists predominantly of an alpha helix, which is intertwined with its partner to form a long tail to the molecule. The head region contains binding sites for actin and for ATP, whereas aggregation with other myosin molecules to form filaments occurs at the tail region. Example from human muscle protein is a hexamer of two heavy chains and four light chains. Different isoforms exist for different muscle types. Light chain 1, skeletal muscle isoform: database code MLE1_HUMAN, 193 amino acids (20.99 kDa); light chain has an **EF hand** motif. Heavy chain, cardiac muscle β isoform: database code MYSB_HUMAN, 1934 amino acids (222.73 kDa); five motifs. Some early preparations of myosin were denoted by letters. Thus myosin A and myosin B were actin-poor and actin-rich preparations respectively, while myosin T and L-myosin wre among the first actin-free preparations. The name myosin was originally given by F. W. Kühne in 1859 to the substance in muscle press juice which on standing at room temperature set to a gel.

myosin-heavy-chain kinase EC 2.7.1.129; an enzyme that

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catalyses the phosphorylation by ATP of specific threonines of myosin heavy chain with release of ADP, during chemotaxis of *Dictyostelium discoideum* (slime mould). It inhibits myosin thick filament formation. Example from *D. discoideum*: database code KMHC_DICDI, 783 amino acids (89.05 kDa).

myosin-light-chain kinase EC 2.7.1.117; *other names*: myosin kinase; smooth-muscle-myosin-light-chain kinase; an enzyme that catalyses the phosphorylation by ATP of myosin light chain with release of ADP. It was one of the first Ca^{2+}/calmodulin-dependent protein kinases to be discovered. Its specificity is restricted to myosin light chain. In skeletal muscle, light-chain phosphorylation modulates tension during contraction. In smooth muscle, it initiates contraction. Examples from chicken: nonmuscle, database code KML2_CHICK, 1258 amino acids (139.56 kDa); muscle, database code KMLC_CHICK, 648 amino acids (73.09 kDa).

myosin-light-chain-phosphatase EC 3.1.3.53; *other names*: myosin light chain kinase phosphatase; myosin phosphatase; an enzyme that catalyses the hydrolysis of phosphate from myosin light-chain phosphate. Example from chicken (large chain, long form): database code A55142, 1004, amino acids (111.48 kDa).

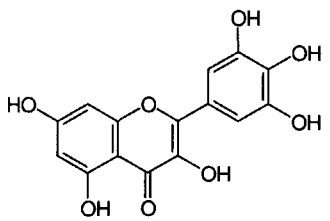
myotonia any genetically distinct hereditary disease characterized by specific muscle malformations.

myotrophin a 12 kDa protein of hypertrophied myocardium of spontaneously hypertensive rats that stimulates protein synthesis in cultured adult rat myocytes *in vitro*. It contains putative consensus phosphorylation sites for protein kinase C and casein kinase II, and binds to **NF-κB**. Example (fragments): database code A37902, 38 amino acids (3.96 kDa).

myotube the multinucleate structure formed by the fusion of proliferating myoblasts in culture under certain conditions. It is characterized by the presence of certain muscle-specific proteins that are not found in the myoblast and may represent a stage in the development of skeletal muscle cells.

Myr *symbol for* the **myristoyl** group.

myricetin 3,3′,4′,5,5′,7-hexahydroxyflavone; a **flavone** that is widely distributed in plants. The name originates from *Myrica*, a genus of shrubs. Myricetin inhibits a number of enzymes, including α-glucosidase, xanthine oxidase, and glyoxalase.



myricyl *or* **melissyl** *the common name for* triacontyl, CH_3–$[CH_2]_{28}$–CH_2–, the alkyl group derived from the C_{30} straight-chain alkane, triacontane. Myricyl palmitate is the major component of beeswax.

myristate **1** *the trivial name for* tetradecanoate, CH_3–$[CH_2]_{12}$–COO^-, the anion derived from myristic acid (i.e. tetradecanoic acid), a saturated straight-chain higher fatty acid and a major component of many plant and animal fats. **2** any mixture of free myristic acid and its anion. **3** any salt or ester of myristic acid.

myristin *an old name for* any of the glyceryl esters of myristic acid, especially the triester, **trimyristin**, or trimyristoylglycerol.

myristoleic acid *see* **tetradecenoic acid**.

myristoyl *or (formerly)* **myristyl** *symbol*: Myr; *the trivial name for* tetradecanoyl, CH_3–$[CH_2]_{12}$–CO–, the acyl group derived from myristic acid (i.e. tetradecanoic acid). It occurs in most animal and plant fats and oils as acylglycerols and in phospholipids. The oils of the seeds of nutmeg (*Myristica fragrans*) and other members of the Myristicaceae are particularly rich sources. *Compare* **myristyl**.

myristoylation the introduction of one or more **myristoyl** groups into an organic compound. Protein *N*-myristoylation refers to the covalent attachment of a **myristoyl** group via an amide bond to the N-terminal Gly residue of a nascent polypeptide. This **post-translational modification** has only been observed in eukaryotes and is irreversible. The *N*-myristoyl proteins are numerous with diverse functions. In some cases the modification is essential for the biological role of the protein, while in other cases it is not essential. The process is catalysed by glycylpeptide *N*-tetradecanoyltransferase (EC 2.3.1.97).

myristyl **1** *the common name for* tetradecyl, CH_3–$[CH_2]_{12}$–CH_2–, the alkyl group derived from tetradecane; use deprecated. **2** *a former trivial name for* tetradecanoyl (**myristoyl** now used).

myrosinase *an alternative name for* **thioglucosidase**.

myt5 the gene for bacteriophage T5 5′-exodeoxynuclease (EC 3.1.11.3). It performs exonucleolytic cleavage in the 5′ to 3′ direction to yield 5′-phosphomononucleotides. Database code EXO5_BPT5, 291 amino acids (33.41 kDa). *See also* **deoxyribonuclease**.

myxamoeba *or (esp. US)* **myxameba** a nonflagellated, naked, ameboid cell that occurs in the life cycle of some slime moulds.

myxedema *or (esp. Brit.)* **myxoedema** the syndrome caused by hypothyroidism in adults. It is characterized by mucoid infiltration and coarsening of the skin, weight gain, intolerance to cold, and mental sluggishness.

myxo+ *or (usually before a vowel)* **myx+** *comb. form* indicating mucoid, mucus, or slime.

Myxobacterales the myxobacteria; an order of Gram-negative bacteria that bear extracellular slime and have a characteristic swarming habit that leads to the formation of stalked fruiting bodies. A more recent classification has suggested replacement of Myxobacterales by Myxococcales.

myxobacteria bacteria belonging to the order **Myxobacterales**.

myxoedema *a variant spelling (esp. Brit.) of* **myxedema**.

myxomatosis a highly contagious disease of rabbits, caused by a myxoma virus, part of a subgenus of poxvirus. It is characterized by proliferative changes in the connective tissues.

Myxomycetes a large class of very primitive organisms, also known as the true or acellular slime moulds, found living saprophytically in damp conditions. Their major vegetative stage is a multinucleate migratory mass of protoplasm, from which (usually macroscopic) fruiting bodies arise.

myxovirus any of a group of negative-strand RNA animal viruses, now divided into **orthomyxoviruses** and **paramyxoviruses**.

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Nn

n *symbol for* **1** nano+ (SI prefix denoting 10^{-9} times). **2** neutron; may be written as n^0 to indicate its charge.

n *symbol for* **1** any (unknown or unspecified) number, especially an integer. **2** amount of substance; the substance in question may be indicated as a suffix in parentheses or by a subscript. **3** refractive index (of a nonabsorbing material); n_D *symbol for* refractive index measured with light of the sodium D-lines (589.0 and 589.5 nm). **4** order of reaction. **5** order of reflection. **6** haploid number of chromosomes. **7** number density.

n- *prefix* indicating normal (isomer); no longer used.

n_H *symbol for* Hill coefficient (alternative to *h*).

N *symbol for* **1** nitrogen. **2** newton. **3** a residue of the α-amino acid L-asparagine (alternative to Asn). **4** a residue of an incompletely specified base in a nucleic-acid sequence that may be adenine, cytosine, guanine, or either thymine (in DNA) or uracil (in RNA). **5** an undetermined, unidentified, or unspecified nucleoside residue (alternative to Nuc). **6** (when suffixed to the symbol for a sugar molecule or residue) aminodeoxy+; e.g. GlcN is the symbol for 2-amino-2-deoxy-D-glucose (i.e. D-glucosamine). **7** normal (def. 1).

N *symbol for* **1** the SI derived physical quantity named number of entities (e.g. molecules, atoms, ions, formula units). **2** neutron number. **3** Avogadro constant (N_A or *L* now recommended). **4** the total number of receptors per unit area of membrane, per cell, or per unit mass of protein.

N- *prefix (in chemical nomenclature)* indicating substitution on nitrogen; a particular nitrogen atom may be specified by a right superscript.

N_A *symbol for* Avogadro constant (alternative to *L*).

N_L *symbol for* Loschmidt constant.

Na *symbol for* sodium.

NA *abbr. for* **1** nicotinic acid. **2** noradrenaline (i.e. **norepinephrine**). **3** nucleic acid. **4** numerical aperture.

NAc *symbol for* (when suffixed to the symbol for a sugar molecule or residue) an acetylated **aminodeoxy sugar**; e.g. GlcNAc is the symbol for *N*-acetylglucosamine or 2-acetamido-2-deoxy-D-glucose.

nactin any of a group of **macrotetrolide** antibiotics produced by various strains of *Actinomyces*. The group includes **nonactin**, monactin, dinactin, and trinactin.

NAD *abbr. for* nicotinamide-adenine dinucleotide (when its oxidation state is unknown or unspecified). *See also* **NAD⁺**, **NADH**, **NADP**, **NAD(P)**.

NAD⁺ *abbr. for* oxidized nicotinamide-adenine dinucleotide.

NAD⁺ ADP-ribosyltransferase *see* **poly(ADP)-ribosyl transferase**.

NADH *abbr. for* nicotinamide-adenine dinucleotide (reduced). Use of $NADH_2$ to represent NADH is not recommended.

NADH dehydrogenase EC 1.6.99.3; *systematic name*: NADH:(acceptor) oxidoreductase; *other names*: cytochrome *c* reductase; type I dehydrogenase. An enzyme that catalyses a reaction between NADH and an acceptor to form NAD^+ and a reduced acceptor; FAD is a coenzyme. The protein contains iron–sulfur complexes. This is a form of **NADH dehydrogenase (ubiquinone)**, the catalytic activity of **complex I** of the mitochondrial respiratory chain that results from isolation procedures. The activity is modified in a way that causes the enzyme to react directly with cytochrome *c* as the acceptor. Example from *Escherichia coli*, membrane protein: database code DHNA_ECOLI, 433 amino acids (47.17 kDa). The enzyme in which the acceptor is a quinone is EC 1.6.99.5; *recommended name*: NADH dehydrogenase (quinone); *systematic name*: NADH:(quinone-acceptor) oxidoreductase; it has no cofactors. In mitochondria, the enzyme is one activity of NADH–ubiquinone oxidoreductase, EC 1.6.5.3; *recommended name*: NADH dehydrogenase (ubiquinone); *systematic name*: NADH:ubiquinone oxidoreductase; *other names*: ubiquinone reductase, type I dehydrogenase, complex I dehydrogenase. This FAD-containing enzyme catalyses the oxidation of NADH by ubiquinone to form NAD^+ and ubiquinol. The protein also contains iron–sulfur complexes. This is the catalytic activity of mitochondrial **complex I**. Example from *Neurospora crassa*, NADH-ubiquinone oxidoreductase 9.6 kDa subunit and NADH dehydrogenase: database code ACP_NEUCR, 134 amino acids (14.44 kDa).

NADH dehydrogenase (ubiquinone) EC 1.6.5.3; *other names*: ubiquinone reductase; type I dehydrogenase; complex I dehydrogenase; a flavoprotein enzyme that catalyses the reaction:

$$\text{NADH} + \text{ubiquinone} = \text{NAD}^+ + \text{ubiquinol}.$$

The flavin is FAD, and the protein also contains iron–sulfur complexes. This is the catalytic activity of mitochondrial **complex I**. Example from *Neurospora crassa*, NADH-ubiquinone oxidoreductase 9.6 kDa subunit and **NADH dehydrogenase**: database code ACP_NEUCR, 134 amino acids (14.44 kDa).

NADH kinase EC 2.7.1.86; an enzyme that catalyses the formation of NADPH from ATP and NADH with release of ADP.

Nadi reagent a mixture of 1-naphthol and *N*,*N*-dimethyl-*p*-phenylene diamine that can be oxidized by cytochrome oxidase to form indophenol blue.

NAD⁺ kinase EC 2.7.1.23; *other name* (*now obsolete*): DPN kinase; an enzyme that catalyses the formation of $NADP^+$ from ATP and NAD^+ with release of ADP.

NADP *abbr. for* nicotinamide-adenine dinucleotide phosphate (when its oxidation state is unknown or unspecified). *See also* **NAD**, **NADP⁺**, **NAD(P)**, **NADPH**.

NADP⁺ *abbr. for* oxidized nicotinamide-adenine dinucleotide.

NAD(P) *abbr. for* a coenzyme that may be NAD or NADP.

NAD(P)⁺ *abbr. for* a coenzyme that may be NAD^+ or $NADP^+$.

NAD(P)⁺–arginine ADP-ribosyltransferase EC 2.4.2.31; *other names*: ADP-ribosyltransferase; mono(ADP-ribosyl) transferase; a sarcoplasmic reticulum enzyme that catalyses the formation of N^2-(ADP-D-ribosyl)-L-arginine from NAD^+ and L-arginine with release of nicotinamide. It couples poly(ADP-ribose) to arginine residues in proteins. Example from rabbit: database code NART_RABIT, 327 amino acids (36.09 kDa).

NADPH *abbr. for* nicotinamide-adenine dinucleotide phosphate (reduced). Use of $NADPH_2$ to represent NADPH is not recommended.

NAD(P)H *abbr. for* a coenzyme that may be either NADH or NADPH. Use of $NAD(P)H_2$ to represent NAD(P)H is not recommended.

NADPH:adrenodoxin oxidoreductase EC 1.18.1.2; *other names*: adrenodoxin reductase; *recommended name*: ferredoxin-$NADP^+$ reductase; a flavoprotein enzyme that catalyses the reaction:

$$\text{reduced ferredoxin} + \text{NADP}^+ = \text{oxidized ferredoxin} + \text{NADPH}.$$

The flavin is FAD. 3-D structure known; it has much α-helical structure and a **beta barrel**. The location of the cofactor binding site is known. Examples (human): database code ADRO_HUMAN, 497 amino acids (54.39 kDa); 3-D structure with 2′-phospho-5′-AMP from spinach: database code NRL_2FNR, 296 amino acids (33.47 kDa).

NAD(P)⁺ stereospecificity in oxidation–reduction reactions involving the nicotinamide coenzymes, NAD^+ and $NADP^+$ reversibly accept hydrogen at the 4 position of the nicotinamide ring. In NADH and NADPH this position is **prochiral**, and the faces of the nicotinamide ring and the C-4 hydrogens of the dihydronicotinamide ring may be labelled according to the

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Re/Si and *pro-R/pro-S* conventions, respectively. Then, if the ring is drawn with the $-CONH_2$ group pointing to the right, the hydrogen projecting out from the plane of the paper is the *pro-R* hydrogen (*or* H_R) and that projecting back the *pro-S* hydrogen (*or* H_S). Alcohol dehydrogenases (EC 1.1.1.1) transfer to the *Re* face (i.e. that from which H_R points out) and use H_R. In biochemistry the *pro-R* hydrogen region is also labelled as H_A, and the *pro-S* hydrogen as H_B. Enzymes that use the *pro-R* hydrogen (H_A) are described as A-specific, while those that use the *pro-S* hydrogen (H_B) are called B-specific. *See also* **pro-R/pro-S convention** and **Re/Si convention**.

NAD(P)$^+$ transhydrogenase (AB-specific) EC 1.6.1.2; *other names*: pyridine nucleotide transhydrogenase; transhydrogenase. An enzyme that catalyses the same reaction as **NAD(P)$^+$ transhydrogenase (B-specific)**; however, preparations from heart mitochondria are A-specific with respect to NAD^+ and B-specific with respect to $NADP^+$. *See also* **NAD(P)$^+$ stereospecificity**.

NAD(P)$^+$ transhydrogenase (B-specific) EC 1.6.1.1; *other names*: pyridine nucleotide transhydrogenase; nicotinamide nucleotide transhydrogenase; a flavoprotein enzyme that catalyses the reaction

$$NADPH + NAD^+ = NADP^+ + NADH$$

(with specificity for H_B of NADPH and NADH). The flavin is FAD. The enzyme is coupled to respiration and acts as a **hydrogen-ion pump**. Example, bovine mitochondrial precursor: NNTM_BOVIN, 1086 amino acids (113.91 kDa). Example, two subunits of enzyme from *Escherichia coli*: α, database code PNTA_ECOLI, 510 amino acids (54.56 kDa); β, database code PNTB_ECOLI, 462 amino acids (48.67 kDa). *See also* **NAD(P)$^+$ stereospecificity**.

NAD+ pyrophosphorylase *see* **nicotinamide-nucleotide adenylyltransferase**.

NAD$^+$ synthase EC 6.3.1.5; *other name*: NAD^+ synthetase; an enzyme that catalyses the formation of NAD^+ from deamido-NAD^+, ATP, and NH_3 with release of AMP and pyrophosphate. *See also* **NAD$^+$ synthase (glutamine-hydrolysing)**; **nicotinamide–nucleotide adenylyltransferase**.

NAD$^+$ synthase (glutamine-hydrolysing) EC 6.3.5.1; *other name*: NAD^+ synthetase (glutamine-hydrolysing); an enzyme that catalyses the formation of NAD^+ from deamido-NAD^+, L-glutamine, ATP, and H_2O with release of AMP, pyrophosphate, and L-glutamate. Example from *Escherichia coli* (also called nitrogen-regulatory protein): database code NADE_ECOLI, 274 amino acids (30.56 kDa). *See also* **nicotinamide–nucleotide adenylyltransferase**.

NAF *abbr. for* Neu-activating factor (*see* **neu**).

NAG *abbr. for N*-acetylglucosamine.

NAGA *abbr. for N*-acetylgalactosamine.

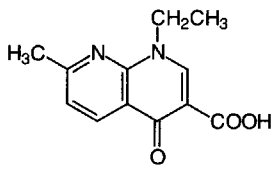
Nagarse (proteinase) *another name for* a species variant of **subtilisin**, EC 3.4.21.62, from *Bacillus subtilis*; an endopeptidase with a broad spectrum of proteolytic activity.

Nagase *a pseudoacronym for β-N*-acetylglucosaminidase (formerly EC 3.2.1.30). This enzyme is now included with EC 3.2.1.52, *β-N*-acetyl-hexosaminidase.

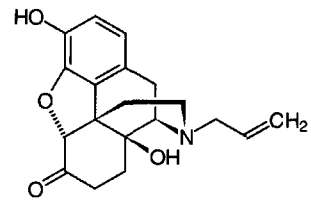
NAIBS *abbr. for* nonadrenergic imidazoline binding site; *see* **imidazoline receptors**.

Na$^+$,K$^+$-ATPase *see* **sodium/potassium ATPase**.

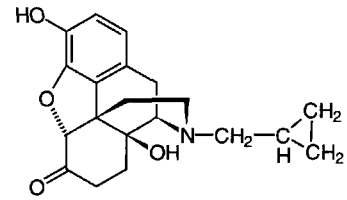
nalidixic acid 1-ethyl-7-methyl-1,8-naphthyridin-4-one-3-carboxylic acid; a synthetic **4-quinolone antibiotic** that is active against many Gram-negative bacteria. It specifically inhibits bacterial DNA gyrase thereby interfering with DNA synthesis. It has no apparent effect on eukaryotic DNA synthesis.



naloxone 1-*N*-allyl-7,8-dihydro-14-hydroxynormorphinone; one of the most effective opiate antagonists. It binds tightly to opiate receptors in the nervous system, its action depending on the 3-carbon side-chain substitution on the nitrogen. It is used as an antidote to overdosage of narcotics.



naltrexone 1-*N*-cyclopropylmethyl-7,8-dihydro-14-hydroxynormorphinone; the cyclopropylmethyl analogue of **naloxone**; it has similar properties but is longer acting.



NANA *abbr. for N*-acetylneuraminic acid (i.e. **sialic acid**).

nano+ *symbol*: n; SI prefix denoting 10^{-9} times. It was formerly known as millimicro (*symbol*: mμ).

nanogram *symbol*: ng; a unit of mass equal to 10^{-9} gram, or 10^{-12} kilogram.

nanometre *or (US)* **nanometer** *symbol*: nm; a unit of length equal to 10^{-9} metre. It was formerly known as millimicron (*symbol*: mμ).

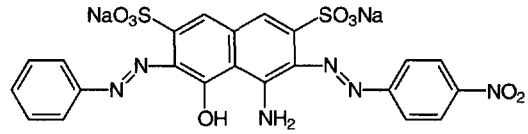
nanomolar *symbol*: nM *or* nM; describing a solution containing one **nanomole** per litre of solution, or a specified multiple or fraction thereof; describing an amount-of-substance concentration similarly expressed.

nanomole *symbol*: nmol; a unit of amount of substance equal to 10^{-9} mole.

nanosecond *symbol*: ns; a unit of time equal to 10^{-9} second.

NAP-2 *abbr. for* neutrophil activating peptide 2; one of several peptides derived from **platelet basic protein precursor**. It consists of **LA-PF4** without the first 15 N-terminal amino acids. It is a potent chemoattractant and activator for neutrophils.

Naphthalene Black *or* **Naphthol Blue Black** *or* **Amido Black** a dye used for staining protein on cellulose acetate or on starch or agarose gels.



Naphthol Blue Black *an alternative name for* **Naphthalene Black**.

Napierian logarithm *symbol*: $\log_e$ *or* ln; *an alternative name for* natural **logarithm**. [After John Napier (1550–1617), Scots mathematician who invented logarithms.]

narcosis a state of partial or complete loss of consciousness induced by a drug or drugs that have a depressant action on the central nervous system.

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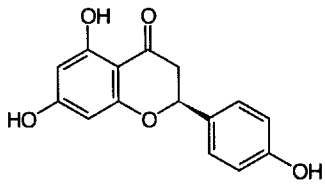
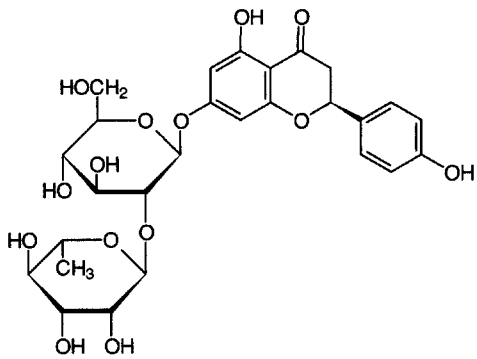
narcotic 1 any of a heterogeneous group of drugs that is capable of inducing narcosis and noted for their analgesic action. 2 *(esp. US) the trivial name for* any illegal drug or abused drug. 3 of, or relating to, narcosis; of, relating to, or denoting a narcotic drug.

naringenin 4′,5,7-trihydroxyflavanone; the aglycon of **naringin**.



S-(–)-enantiomer

naringin naringenin-7-rhamnoglucoside; a compound that occurs in the flowers, fruit, and rind of the grapefruit, and is the main bitter component of grapefruit juice. *See also* **naringenin**.



nascent just formed or in the process of being formed, especially in a chemical or biochemical reaction.

Nathans, Daniel (1928–), US microbiologist and molecular biologist; Nobel Laureate in Physiology or Medicine (1978) jointly with W. Arber and H. O. Smith 'for the discovery of restriction enzymes and their application to problems of molecular genetics'.

native *(of a biopolymer)* undenatured, i.e. having the structure and biological activity possessed in living material.

native state of a protein or nucleic acid, the form in which it occurs in the intact cell, its three-dimensional structure depending on formation of the appropriate hydrogen bonds.

natriuresis the excretion of sodium ions in the urine.

natriuretic 1 describing any agent that promotes the excretion of sodium ions in the urine. 2 such an agent.

natriuretic hormone any of various substances present in plasma or urine that are capable of stimulating sodium excretion by the kidney and of inhibiting membrane Na^+,K^+-ATPase in cells from kidney and some other tissues. *See* **natriuretic peptide**.

natriuretic peptide any of several peptides, secreted by various tissues, that stimulate natriuresis. The first of the group to be identified was **atrial natriuretic peptide** (*or* atrial natriuretic factor) (*abbr.*: ANP; *other name*: type A natriuretic peptide; *former names*: atriopeptin; vasoactive peptide). Its discovery arose from the observation that extracts of atrial granules could bring about **natriuresis**. Subsequently, **brain natriuretic peptide** (*abbr.*: BNP; *other name*: type B natriuretic peptide) and **type C natriuretic peptide** (CNP) were identified. Members of this family share many common features; they are produced primarily in the heart and specialized areas of the central nervous system, and induce diuresis, natriuresis, and vasorelaxation. The natriuretic effect results from direct inhibition of sodium absorption in the collecting duct, increased glomerular filtration, and inhibition of aldosterone production and secretion. The major constituent of atrial granules, ANP, is synthesized from a precursor, prepronatriodilatin (152 amino acids), which is cleaved to proANP (126 amino acids). The latter is strikingly homologous between many species; proANP is cleaved into an N-terminal fragment, amino-acid residues 1–98, and the biologically active hormone, residues 99–126; the amino-acid sequence of ANP (proANP 99-126) is identical in all mammalian species except at residue 12 (110 of proANP), which is methionine in humans, dogs, and cows but isoleucine in rats, mice, and rabbits. There are two genes for the precursor (prepronatriodilatin); cleavage of the latter leads to two peptides, ANP:

SLRRSSCFGGRMDRIGAQSGLGCNSFRY

and cardiodilatin-related peptide (CDP):

NPMYNAVSNADLMDFKNLLDHLEEKMPLED.

The synthesis of BNP follows a very similar course. In humans and pig a 32-amino-acid hormone is the circulating form of BNP, sequence (human)

SPKMVQGSGCFGRKMDRISSSSGLGCKVLRRH;

in rodents BNP contains 45 amino acids and is known as iso-ANP. A 17-member ring, formed by a disulfide bridge between the two cysteine residues, is essential for biological activity of ANP and BNP. *See also* **natriuretic-peptide receptor**.

natriuretic-peptide receptor any of several membrane proteins that bind **natriuretic peptides** and mediate their intracellular effects. Three receptors have been identified by molecular cloning: ANP_A (previously known as GC-A, ANP-R_1, or ANP_B); ANP_B (previously known as GC-B); and ANP_C. Human ANP_A and ANP_B each have one transmembrane domain and intrinsic guanylate cyclase activity in an intracellular domain, which is highly conserved (88% identity). At the ANP_A receptor, atrial natriuretic peptide is about ten times more potent than brain natriuretic peptide, whereas type C natriuretic peptide is 50–500 times more potent than other agonists at the ANP_B receptor. ANP_C is a disulfide-linked homodimer with one transmembrane domain and no guanylate cyclase domain; it was once thought to be involved in clearance of natriuretic peptides, but may act through other second messenger systems. Examples from human; ANP_A receptor: database code ANPA_HUMAN, 1061 amino acids (117.78 kDa); ANP_B receptor: database code ANPB_HUMAN, 1047 amino acids (116.88 kDa); ANP_C receptor: database code ANPC_HUMAN, 540 amino acids (59.70 kDa). All are type I membrane glycoproteins.

natural abundance the number of atoms of a given nuclide in any naturally occurring mixture of the nuclides of a particular element, expressed as a percentage or fraction of the total number.

natural killer cell *see* **NK cell**.

natural logarithm *or* **Napierian logarithm** *symbol*: $\log_e$ *or* ln; *see* **logarithm**.

natural product any organic substance of biological origin, as opposed to one obtainable only by chemical synthesis. In practice the term is often restricted to mean **secondary metabolite**.

natural selection the principle that the best competitors in any given population of organisms have the best chance of breeding success and thus of transmitting their characteristics to subsequent generations. The members of any population show individual differences – anatomical, physiological, or metabolic – that affect their functional efficiency in a given environment. The less efficient members tend to die out or produce fewer offspring than the more efficient members, which are better adapted to compete for food or other resources, and so produce relatively more offspring. The principle is fundamental to modern concepts of evolution, and was first articulated, independently, by the British naturalists Alfred Russel Wallace (in 1858) and Charles Darwin (in 1859).

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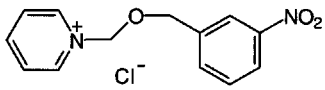
natural-selection theory of immunity *or* **Jerne's theory of immunity** a theory of antibody production that postulates the spontaneous presence, in the blood of an animal, of small numbers of antibody molecules against all antigens to which the animal can respond, and delegates to the antigen the sole role of carrying such specific globulin molecules from the bloodstream into cells in which these molecules can induce proliferation of a particular antibody.

Nb *symbol for* niobium.

NBPC *abbr. for* 1-[(*m*-nitrobenzyloxy)methyl]pyridinium chloride; a reagent useful for the immobilization of single-stranded nucleic acids on cellulose.



NBS *abbr. for* **1** National Bureau of Standards (of the USA) (now National Institute for Standards and Technology). **2** *N*-bromosuccinimide.

NCAM *abbr. for* neural cell adhesion molecule.

N cell a type of cell, found mainly in the upper small intestine in humans, that contains round, homogeneous granules in which **neurotensin** is stored. Such cells are sparse in the lower small intestine.

NC-IUB *abbr. for* Nomenclature Committee of the International Union of Biochemistry; redesignated (in 1992) **NC-IUBMB**.

NC-IUBMB *abbr. for* Nomenclature Committee of the International Union of Biochemistry and Molecular Biology. *Compare* **JCBN**.

NCS *the proprietary name for* a 0.6 M solution in toluene of a mixture of quaternary ammonium compounds of general formula $[(CH_3)_2R'R''N]^+OY^-$, where R′ and R″ are unbranched alkyl groups containing 6 to 20 carbon atoms and Y is a hydrogen atom or a lower alkyl group. It is useful for solubilizing a wide range of specimens of biological origin in organic solvents for liquid scintillation counting.

Nd *symbol for* neodymium.

nDNA *abbr. for* nuclear DNA.

NDP *abbr. for* any (unknown or unspecified) nucleoside diphosphate in which the diphosphate moiety is esterified at the 5′ position of the glycose.

Ne *symbol for* neon.

NE *abbr. for* norepinephrine.

nearest-neighbour sequence analysis a technique that employs a 5′-^{32}P-labelled deoxyribonucleotide substrate in the enzymic synthesis of DNA followed by enzymic degradation of the DNA specifically to 3′-deoxyribonucleotides. From knowledge of the labelled substrate used and of the labelled degradation products formed, the **nearest neighbour frequency**, i.e. the frequency with which a particular nucleotide is found next to a specific neighbour nucleotide in the polynucleotide chain, can be calculated.

near ultraviolet radiation **ultraviolet radiation** in the wavelength range 200–400 nm.

nebulin a giant protein (800 kDa) that is specific for the skeletal muscle of vertebrates; it acts possibly as a 'molecular ruler' for length regulation of the thin filament. The protein appears to have small repeats of approximately 35 amino acids. Example, partial sequence (241 amino acids) from human: database code NEBU_HUMAN.

nebulize *or* **nebulise** to convert a liquid into a mist or a spray of fine droplets. —**nebulization** *or* **nebulisation** *n.*

nebulizer *or* **nebuliser** a device for nebulizing a liquid (*see* **nebulize**); an atomizer.

necrobiosis the death of a cell or a group of cells within a tissue, whether a normal occurrence or due to a pathological process.

necropsy *another name for* **autopsy**.

necrosis the death of a portion of a tissue as a result of disease or injury.

nectary a gland that secretes the sugary fluid called nectar. Nectaries occur in many animal-pollinated flowers, to attract insects, birds, and other pollinating agents.

Nedd *abbr. for* NPC-expressed, developmentally down-regulated genes (NPC is an abbreviation of neural precursor cells). These genes were isolated as DNA corresponding to mRNA, the levels of which are down-regulated during mouse brain development. The products are proteins presumed to be involved in embryonic development and differentiation of the nervous system. Nedd-2 protein is a cysteine endopeptidase that may be involved in controlling cell death. Example, Nedd-2 from mouse: database code NED2_MOUSE, 171 amino acids (19.22 kDa).

Needham, Joseph (1901–95); British biochemist, embryologist, Sinologist, and science historian, noted for his multivolume *Science and Civilization in China* (now being continued by the Needham Research Institute, Cambridge, UK). During World War II, he proposed the formation of an international science agency, and was credited with putting the S (science) into UNESCO.

NEFA *abbr. for* nonesterified fatty acid. *Compare* **FFA**.

negative **1** (of an electric charge) having the same polarity as an electron. **2** (of a chemical entity) having a negative electric charge; having an excess of electrons. **3** (of a point in an electric circuit) having a lower potential than some other point to which a potential of zero is assigned. **4** *(in photography)* an exposed and developed photographic film or plate showing an image in reversed tones, or complementary colours, to those of the object photographed. **5** a quantity less than zero. —**negativeness** *or* **negativity** *n.*

negative chromatography *a term sometimes used to denote* methods of purification of substances by **affinity chromatography** in which a specific contaminant in a sample interacts with and is selectively retained by the adsorbent, especially as opposed to **positive chromatography**.

negative-contrast technique a technique used in preparing specimens for electron microscopic examination in which the specimen is mixed with an electron-dense material that penetrates the interstices of the specimen but not the material of the specimen itself. The specimen thus appears transparent against an opaque background. It is commonly called **negative staining**.

negative control the prevention of some biological activity caused by the presence of a specific chemical entity.

negative cooperativity a form of **cooperative ligand binding** in which binding of one ligand to one site on a (macro)molecule decreases the affinity at other sites for the subsequent binding of other ligands.

negative effector *see* **effector**.

negative feedback *see* **feedback** (def. 1).

negative-ion mass spectrometry a version of **mass spectrometry** in which negative rather than positive ions, generated from the sample by chemical ionization, are separated and measured in an appropriate instrument.

negative staining *see* **negative-contrast technique**.

negative strand *another name for* **minus strand** (def. 2); in some RNA viruses, RNA is a minus strand which does not directly code for protein. Such viruses have a replicase packaged into the capsid to enable them to synthesize the plus strands necessary for replication.

negative-strand virus *or* **negative-stranded virus** any RNA virus in which the genome consists of single-stranded RNA (i.e. minus strand) of base sequence complementary to that of the virus-specified mRNA (which is the positive, or plus, strand). Such viruses, which comprise class V in the **Baltimore classification**, must make a positive RNA strand before making viral proteins. *See also* **minus strand** (def. 2), **plus strand** (def. 2).

Neher, Erwin (1944–), German biophysical chemist; Nobel Laureate in Physiology or Medicine (1991) jointly with B. Sakmann 'for their discoveries concerning the function of single ion channels in cells'.

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NEM *abbr. for N*-ethylmaleimide.

nematic (of a substance) being in or having a mesophilic state in which the molecules are arranged as in a series of parallel threads but not in layers. The molecules can rotate about their axes and can move in the plane orthogonal to the line of the thread. *Compare* **smectic**. *See also* **liquid crystal**.

Nembutal *a proprietary name for* pentobarbitone sodium; pentobarbital sodium.

N-end rule a rule stating that the *in vivo* half-life of a protein is a function of its N-terminal residues.

NENTREZ a version of **ENTREZ** for use on individual personal computers. It is available on a licensing basis free of charge to academic researchers.

neo+ *comb. form* **1** denoting new, recent. **2** *(in chemistry)* denoting an isomer of new (and therefore initially unknown) structure.

neo-Darwinism the reworking of evolutionary theory in the light of discoveries about genetics as a result of the work of Fisher, Haldane, Sewall Wright, and others. The behaviour of genes in natural populations is understood in terms of the four fundamental evolutionary forces: **natural selection**, **genetic drift**, gene flow, and **mutations**.

neoendorphin any of a small group of [Leu^5]enkephalin-related peptides. α Neoendorphin is the decapeptide [Leu^5]enkephalinyl-Arg-Lys-Tyr-Pro-Lys, and β neoendorphin is the nonapeptide [Leu^5]enkephalinyl-Arg-Lys-Tyr-Pro; both are hypothalamic opioid peptides. *See also* **proenkephalin**.

neoflavone any of a group of 4-phenyl-1,2-benzopyrones found in certain plants. Their occurrence is probably restricted to the Guttiferae and Leguminosae. **—neoflavonoid** *n.*

neoglycoprotein *a proposed generic name for* any originally carbohydrate-free protein that has been chemically derivatized by covalent attachment of carbohydrate.

neokestose *O*-β-D-fructofuranosyl-(2→6)-α-D-glucopyranosyl-β-D-fructofuranoside; an isomer of **kestose** isolated from the sap of the sugar maple and produced artificially, together with kestose, by the action of yeast or mould invertase preparations on sucrose.

neolignan any of a class of phenylpropanoid dimers in which the phenylpropane units are linked head-to-tail instead of tail-to-tail as in **lignans**; e.g. eusiderin from the heartwood of members of the Magnoliaceae.

neomycin an aminocyclitol antibiotic complex produced by *Streptomyces fradiae*. It is made up of three components: neomycin A (*or* **neamine**; a degradation product of neomycin B and neomycin C), neomycin B, and neomycin C. Neomycin causes misreading during protein synthesis in bacteria but its target site on the ribosome is apparently different from that of streptomycin. *See also* **neosamine C**.

neonatal of, relating to, or affecting a newborn animal. For human infants the neonatal period is considered to be the first month after birth.

neonate any newborn animal.

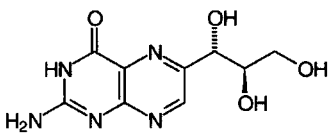
neoplasia **1** the formation of a **neoplasm** or neoplasms. **2** the formation of new tissue.

neoplasm any new and morbid formation of tissue; a tumour.

neoplastic of, or relating to, neoplasia or to a neoplasm.

neoprene poly(2-chloro-1,3-butadiene); a synthetic rubber that is resistant to oils and organic solvents and is useful for the manufacture of flexible tubing, washers, etc. for laboratory and many other uses.

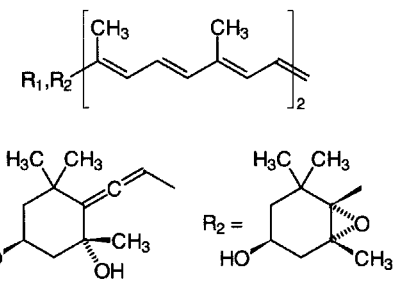
neopterin the D-*erythro* enantiomer of **biopterin**; its biosynthetic precursor.



neosamine C 2,6-diamino-2,6-dideoxy-D-glucose; a constituent of **neomycin** C and some other antibiotics including **kanamycin**.

neosome the suggested secondary particulate biogenic precursor of the ribosome, intermediate between the **eosome** and the completed ribosome. Neosomes in *Escherichia coli* are particles of at least two kinds, with sedimentation coefficients of 43S and 30S.

neoxanthin a carotenoid **xanthophyll** present in the leaves of all higher plants.



nephelometry a technique in which the light dispersed by a suspension is measured orthogonally to the direction of the incident light; the amount of scattered light is dependent on the number and size of the particles in the light path. *Compare* **turbidimetry**. **—nephelometric** *adj.*; **nephelometrically** *adv.*

nephr+ *a variant form of* **nephro+** *(before a vowel)*.

nephrectomy the surgical removal of one or both kidneys. **—nephrectomize** *vb.*

nephro+ *or (before a vowel)* **nephr+** *comb. form* denoting kidney or kidneys.

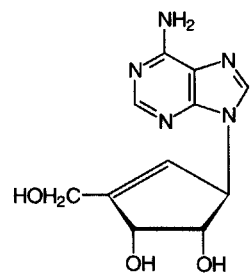
nephrocalcin *or* **osteocalcin-related protein precursor** a calcium-binding protein found in bone. It is expressed only in kidney and is also found as a urinary acidic glycoprotein of humans and other mammals that strongly inhibits formation of calcium oxalate crystals in renal tubules. It contains γ-carboxyglutamic acid residues; a modified protein lacking these is found in patients with calcium oxalate renal calculi. Example from *Mus musculus*: database code OSTR_MOUSE, 95 amino acids (10.46 kDa).

nephrogenic diabetes insipidus a rare X-linked recessive genetic disorder involving renal insensitivity to vasopressin resulting in polyuria and polydipsia; it can also be acquired as a result of toxic damage to the tubules. The genetic form is associated with mutations in the V_2 receptor (*see* **vasopressin receptor**), two examples being substitution of Asp for Ala at position 132 and a frameshift mutation at position 246 leading to a premature stop codon and a truncated receptor.

nephron any of the structural and functional urine-secreting units that occur in the kidney. Typically each nephron is made up of a glomerulus, a proximal convoluted tubule, a loop of Henle, and a distal convoluted tubule.

nephropontin *see* **osteopontin**.

neplanocin A a cyclopentenyl analogue of adenosine; a natural



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antibiotic that inhibits *S*-adenosylhomocysteine hydrolase and vaccinia virus multiplication.

neprilysin EC 3.4.24.11; *other names*: neutral endopeptidase; endopeptidase 24.11; enkephalinase; a zinc endopeptidase widely distributed on the outer surfaces of cells.

Ner *symbol for* the nervonoyl (i.e. (*Z*)-tetracos-15-enoyl) group.

Nernst, Walther Hermann (1864–1941), German physical chemist distinguished for his work on thermochemistry and chemical thermodynamics; Nobel Laureate in Chemistry (1920) 'in recognition of his work in thermochemistry'.

Nernst distribution law when, at a constant temperature, a solute distributes itself between two immiscible phases, then the ratio of its concentrations in the two phases is constant, and is described by the relation $C_1/C_2 = K$, where C_1 and C_2 are, respectively, the amount-of-substance concentrations of the solute in phases 1 and 2 at equilibrium, and K is the distribution constant. The law only applies in dilute solution.

Nernst equation **a** the potential, E, of an electrode reversible to one ion in a solution containing that ion is given by:

$$E = E^{\circ} + (RT/zF)\ln a,$$

where E° is the standard potential of the electrode (relative to the standard hydrogen electrode), a is the activity of the ion to which the electrode is reversible, z is the charge number of the ion, R is the (molar) gas constant, F is the Faraday constant, and T is the thermodynamic temperature. This equation can be extended to the e.m.f. of an electrolytic cell. **b** For a redox reaction, the potential of an electrode (usually platinum or gold) immersed in a redox solution, E_h, is given by:

$$E_h = E^{\circ} + (RT/nF)\ln(a_{ox}/a_{red}),$$

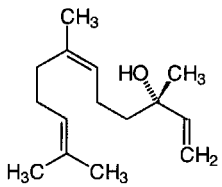
where E° is the standard redox potential of the system at a given pH (usually pH 7.0), n is the number of electrons transferred in the reaction, and a_{ox} and a_{red} are respectively the activities of the oxidized and reduced species in the solution. **c** If two solutions are separated by a membrane permeable to only one of two (or more) ions and the activities of the ions are different on either side of the membrane then a membrane potential, E_A, will be generated where

$$E_A = (RT/zF)\ln(a_L/a_R),$$

where a_L and a_R are the activities respectively of the permeable ion on the left and right sides of the membrane.

Nernst heat theorem *another name for* a particular formulation of the third law of thermodynamics (*see* **thermodynamics**).

nerolidol peruviol; 3,7,11-trimethyl-1,6,10-dodecatrien-3-ol; a widespread acyclic sesquiterpene.



(*S*)-(+)-(*Z*)-enantiomer

nerve any of the cordlike bundles, consisting of **nerve fibres** and **glia** encased in a connective-tissue sheath, that connect the central nervous system to other parts of the body. They may be motor, sensory, or of mixed function.

nerve cell *an alternative name for* **neuron**.

nerve fibre the axonal process of a **neuron** together with its covering sheath. Bundles of nerve fibres running together make up a **nerve**.

nerve gas any of various poisonous gases or volatile liquids that act by inhibiting the passage of impulses through the nervous system and neuromuscular junctions. They are commonly irreversible inhibitors of **acetylcholinesterase**.

nerve growth factor **1** any of a number of polypeptides that exert a trophic effect on neurons. They play a part in the development and maintenance of sensory neurons in dorsal root ganglia and sympathetic neurons in peripheral sympathetic ganglia. **2** *abbr.*: NGF; the first known member of a family of polypeptides that act as growth factors for neurons. In addition to the general properties of such nerve growth factors, it also stimulates growth and differentiation of **B** lymphocytes, and stimulates histamine release from mast cells. The biologically active form of NGF contains two identical polypeptide chains of 120 amino-acid residues and known sequence and exerts its action through specific receptors in the neuronal plasma membrane. It is produced by neurons, astrocytes, and Schwann cells, but also by fibroblasts, epithelial cells, activated macrophages, and smooth muscle cells. It exists as an inactive complex of two α subunits, two β subunits, and two γ subunits. The active form consists of the two β subunits, and is known as βNGF. Example: βNGF precursor, a homodimer, from human: database code NGF_HUMAN, 241 amino acids (26.96 kDa); four motifs; residues 122–241 comprise the homodimer subunit. Related proteins subsequently discovered include **brain-derived neurotrophic factor** and **neurotrophins**.

nerve growth factor receptor any of a family of plasma membrane integral proteins that bind nerve growth factors. Low-affinity and high-affinity binding is observed; high affinity binding, and action on effector systems, requires the presence of both the ***trk*** protooncogene product ($p140^{prototrk}$) and a 75 kDa low affinity receptor glycoprotein ($p75^{NGFR}$). The latter can bind **nerve growth factor** (def. 2), **brain-derived neurotrophic factor**, and **neurotrophins** 3 and 4, but it is apparent that considerable specificity exists in transduction of the signal depending on which member of the nerve growth factor family and which cell type is involved. Example: $p75^{NGFR}$, human precursor, homodimer linked by disulfide bonds, *N*- and *O*-glycosylated; database code NGFR_HUMAN, 427 amino acids (45.13 kDa, increased by glycosylation).

nerve impulse *see* **impulse** (def. 3).

nervon *or* **nervone** the **galactocerebroside** in which the acyl group is **nervonoyl**. It was originally isolated from nervous tissue.

nervonate **1** *numerical symbol*: 24:1 (15); *the trivial name for* (*Z*)-tetracos-15-enoate, $CH_3–[CH_2]_7–CH=CH–[CH_2]_{13}–COO^-$ (*cis* isomer), the anion derived from nervonic acid, (*Z*)-tetracos-15-enoic acid a monounsaturated straight-chain higher fatty acid. **2** any mixture of free nervonic acid and its anion. **3** any salt or ester of nervonic acid. *See also* **nervonoyl**.

nervonoyl *symbol*: Ner; *the trivial name for* (*Z*)-tetracos-15-enoyl, $CH_3–[CH_2]_7–CH=CH–[CH_2]_{13}–CO–$ (*cis* isomer), the acyl group derived from nervonic acid, (*Z*)-tetracos-15-enoic acid. It occurs as the acyl moiety of the cerebroside **nervon** in brain, as a major constituent of milk phosphatidylcholines and sphingolipids in, e.g., pig and human, and in sphingolipids of other tissues.

nervous of, pertaining to, mediated by, or containing nerves; neural.

nervous system the extensive network of cells specialized to carry information, in the form of nerve impulses, to and from all parts of the body. Nervous systems occur in all orders of multicellular animals other than sponges.

nervous tissue tissue from any part of the nervous system.

nesidioblast a precursor cell of a pancreatic islet cell.

nesidioblastoma a tumour of nesidioblasts.

nesidioblastosis a pathological condition in which individual blastic pancreatic duct cells differentiate abnormally into islet cells scattered among the exocrine tissue. The condition is sometimes associated with severe infantile hyperinsulinism and hypoglycemia.

nesslerize *or* **Nesslerize** to treat (a sample) with **Nessler's reagent**; to test for or estimate (ammonia) by such means. *Also*: **nesslerise**, **Nesslerise**. —**nesslerization** *or* **nesslerisation** *n*.

Nessler's reagent an alkaline aqueous solution of potassium tetraiodomercurate(II). It gives a yellow or brown colour or

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precipitate when added to solutions containing ammonia or ammonium ions and is useful in the detection and quantitative estimation of microgram quantities of ammonia in aqueous solution. [After Julius Nessler (1827–1905), German agricultural chemist.]

nestin an intermediate-filament protein whose name derives from neuroepithelial stem cells, in which it is specifically expressed. It has significant homology, including heptad repeats, to other intermediate-filament proteins. Example from rat: database code NEST_RAT, 1805 amino acids (198.53 kDa).

netrin any of a family of proteins first isolated from chick brain as diffusible chemoattractants that guide commissural axons to their targets during development. Netrin 1 is expressed at high levels in the floor plate during the period when commissural axons are growing towards the floor plate, while netrin 2 is similarly expressed at lower levels in the ventral two-thirds of the spinal chord. D nectrin is a *Drosophila* homologue, expressed in midline cells of the central nervous system when commissures are forming. The proteins are related to Unc proteins (e.g. *see* ***unc-86***) of the nematode *Caenorhabditis elegans*.

netropsin a *Streptomyces*-derived basic peptide antibiotic that selectively binds to A–T base pairs in the small groove of right-handed B conformations of DNA. It induces A to B conformational changes in DNA.

net sensitivity *see* **flux control coefficient**.

net synthesis increase in the total mass (of a reaction product), as opposed to any apparent increase estimated by incorporation of labelled precursor (which may arise from exchange).

neu an oncogene first described in association with a neuroblastoma after treatment of rats with ethylnitrosourea. The *neu* protooncogene (also known as c-*erbB2*, *NGL*, and *HER2*) encodes a 185 kDa transmembrane glycoprotein with intrinsic tyrosine kinase activity, related to but distinct from the **epidermal growth factor receptor** (EGFR). Example from rat: database code NEU_RAT, 1260 amino acids (139.03 kDa). Like other members of this receptor family, the *neu* gene product, Neu, possesses a cysteine-rich extracellular domain, a transmembrane domain, and an intracellular domain with tyrosine kinase activity. EGF does not bind to Neu, but a factor known as **Neu-activating factor** (NAF) binds specifically to Neu and will bind to EGFR. Neu was originally identified in brain, and may play a critical role in neurogenesis. The rat *neu* oncogene is activated via a single point mutation in the transmembrane domain, which results in constitutive activation of the tyrosine kinase domain. A similar mutation has not been found in the human *neu* oncogene, the association of which with human cancer through gene amplification, or overexpression of the protein product, has been supported by work with breast and ovarian cancer.

Neu **1** *symbol for* a residue (or sometimes a molecule) of **neuraminic acid**. **2** the product of the ***neu*** gene.

NeuAc *or (formerly)* **AcNeu** *symbol for* a residue (or sometimes a molecule) of any isomer of acetylneuraminic acid, i.e. **sialic acid**. *See also* **NeuNAc**, **NeuOAc**, **neuraminic acid**.

Neu-activating factor *see* ***neu***.

Neuberg, Carl Alexander (1877–1956); German biochemist after whom three forms of fermentation are named.

Neuberg ester *an old name for* D-fructose 6-phosphate. *See* **fructose 6-phosphate**.

Neuberg's first form of fermentation the normal anaerobic ***alcoholic fermentation*** of carbohydrate by yeast to yield two moles each of ethanol and carbon dioxide per mole of glucose fermented.

Neuberg's second form of fermentation the anaerobic fermentation of carbohydrate by yeast in the presence of sodium hydrogen sulfite. The acetaldehyde formed normally, which would act as a hydrogen acceptor for the reoxidation of NADH, is trapped as its bisulfite addition product, and its place is taken by dihydroxyacetone phosphate (i.e. glycerone phosphate), which is reduced to *sn*-glycerol 3-phosphate; this is then dephosphorylated to glycerol. Thus one mole each of glycerol, acetaldehyde–bisulfite complex, and carbon dioxide is formed per mole of glucose fermented.

Neuberg's third form of fermentation the anaerobic fermentation of carbohydrate by yeast in alkaline conditions. The acetaldehyde formed normally, which would act as a hydrogen acceptor for the reoxidation of NADH, undergoes a **Cannizzaro reaction** to form acetic acid and ethanol, and its place is taken by dihydroxyacetone phosphate (e.g. glycerone phosphate), which is reduced to *sn*-glycerol 3-phosphate; this is then dephosphorylated to glycerol. Thus one mole each of glycerol and carbon dioxide, and one half mole each of ethanol and acetic acid, are formed per mole of glucose fermented.

NeuGc *symbol for* a residue (or sometimes a molecule) of *N*-glycoloylneuraminic acid. *See also* **sialic acid**.

NeuNAc *or* **Neu5Ac** *symbol for* a residue (or sometimes a molecule) of *N*-acetylneuraminic acid (i.e. **sialic acid**). It is used as an alternative to NeuAc to differentiate the *N*-acetyl from the *O*-acetyl derivative of neuraminic acid.

NeuOAc *symbol for* a residue (or sometimes a molecule) of *O*-acetylneuraminic acid. It is used as an alternative to NeuAc to differentiate the *O*-acetyl from the *N*-acetyl derivative of neuraminic acid. *See also* **sialic acid**.

neur+ *a variant form of* **neuro+** *(before a vowel)*.

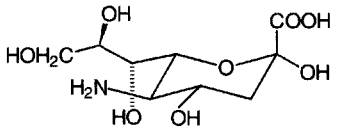
neural of, or pertaining to, a nerve or nerves, or to the nervous system.

neural cell adhesion molecule *abbr.*: NCAM; any of a family of type I membrane glycoproteins of the immunoglobulin superfamily that are involved in neuron–neuron adhesion, neurite fasciculation, outgrowth of neurites, etc. Example (precursor) of NCAM-L1 from human: database code CAML_HUMAN, 1257 amino acids (139.77 kDa); it shows strong homology with a *Drosophila* protein, **neuroglian**.

neural crest a group of embryonic cells, derived from the roof of the neural tube, that migrate to different locations and give rise to various types of adult cells.

neuraminate **1** the anion derived from **neuraminic acid**. **2** any salt or ester of neuraminic acid.

neuraminic acid *symbol*: Neu; the monosaccharide 5-amino-3,5-dideoxy-D-*glycero*-D-*galacto*-nonulosonic acid; it may be regarded as the aldol-condensation product of pyruvic acid and *N*-acetyl-D-mannosamine. It is not found free in nature, but is the parent structure of a family of aminodeoxysugars containing nine or more carbon atoms that occur widely, especially in glycoproteins and gangliosides; they include the **sialic acids**.



α-anomer

neuraminidase *a former name for* **sialidase**.

neuraminosyl *a trivial name for* the glycosyl group derived from **neuraminic acid** by removal of the hydroxyl group from the anomeric carbon atom of the cyclic structure.

neuraminoyl *a trivial name for* the acyl group derived from **neuraminic acid** by removal of the hydroxyl group from the carboxyl group.

neuregulin any member of a family of closely related proteins implicated as regulators of neural and muscle development, and the differentiation and oncogenic transformation of mammalian epithelia. They include the Neu differentiation factor (*see* ***neu***) and the **heregulins**. They exert their effects through

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binding to and activating receptors of the ErbB2/Neu receptor family. Neuregulins stimulate proliferation of Schwann cells, increase the rate of synthesis of acetylcholine receptors in cultured muscle cells, and are concentrated at nerve–muscle synapses.

neurexin any of a family of cell-surface receptors expressed from two genes in the brain and concentrated in neurons. They are cell-surface proteins implicated in axon guidance and synaptogenesis. Some are probably signalling molecules. They are highly polymorphic and include secreted variants. They contain single transmembrane regions and extracellular domains with repeat sequences similar to those in laminin A (*see* **laminin**) and **agrin**. Each gene contains two independent promoters so that transcription produces two classes of mRNA, which encode proteins with different N termini, the larger being referred to as α-neurexins and the shorter as β-neurexins. The former contain three epidermal growth factor domains, an O-linked sugar domain, a transmembrane domain, and a short cytoplasmic tail. The α- and β-neurexins differ in their N-terminal sequences but have identical C termini, including the sugar-rich, transmembrane, and cytoplasmic domains. Example, neurexin III-α from female Sprague–Dawley rat brain: database code RATNIIIA5, 1399 amino acids (154.09 kDa).

neurilemma *or* **neurolemma** the thin outer sheath of cells surrounding the axon (and myelin sheath) of larger peripheral nerves or surrounding the axoplasm of unmyelinated nerves.

neurite *a general term for* a dendrite or an axon.

neuro+ *or (before a vowel)* **neur+** *comb. form* denoting a nerve or the nervous system.

neuroactive (of an agonist or antagonist) having an effect on the nervous system.

neurocalcin an **EF-hand** Ca^{2+}-binding protein involved in the calcium-dependent regulation of rhodopsin phosphorylation and found in retina and brain neurons. Example (bovine): database code NECX_BOVIN, 192 amino acids (22.09 kDa).

neurochemistry the study of the chemical composition of, and the chemical reactions occurring in, nervous tissue. —**neurochemical** *adj.*

neurocrine **1** describing or relating to a neuron that secretes an agonist into a synapse with another neuron; describing or relating to such an agonist. **2** such an agonist, e.g. a **neurotransmitter**.

neuroendocrine **1** describing or relating to a neuron that secretes an agonist into the bloodstream; describing or relating to such an agonist. **2** such an agonist; a **neurohormone**.

neuroendocrine convertase EC 3.4.21.93; *abbr.*: NEC; *other name* prohormone convertase. Any of the enzymes that act at paired dibasic amino acids in precursors of hormones and other **polyproteins**, to cleave the precursor into individual mature proteins. The catalytic activity depends on the Asp-His-Ser **charge-relay system**. Substrates for NEC1 include **proopiomelanocortin**, **renin**, **enkephalin**, **dynorphin**, **somatostatin**, and **insulin**. NEC2 and NEC3 have also been described. Example from human (NEC1 precursor): database code NEC1_HUMAN, 753 amino acids (84.12 kDa).

neuroendocrinology the study of the interrelations between the nervous system and the endocrine system. —**neuroendocrinological** *adj.*

neurofascin a chick neurite-associated glycoprotein implicated in axon extension; it is an axonal surface recognition molecule of the immunoglobulin superfamily. At the N terminus it has six immunoglobulin-like motifs, followed by four fibronectin type III motifs, a proline-alanine-threonine-rich region, a transmembrane domain, and a 113-residue cytoplasmic domain. Example from chicken: database code S26180, 1272 amino acids (142.08 kDa).

neurofibril any of the very fine fibres, visible by light microscopy, that occur in the cell bodies, axons, and dendrites of neurons.

neurofibromatosis any of a number of disorders associated with the presence of multiple **neurofibromas**, benign tumours consisting of a mixture of Schwann cells and fibroblasts. *See also* **neurofibromin**.

neurofibromin *other name*: neurofibromatosis-related protein (NF-I); a GTPase activating protein (*see* **GAP** (def. 2)), the product of the *Nf1* tumour-suppressor gene, that stimulates the GAPase activity of the ***RAS*** oncogene product, thus inactivating it. It appears to be implicated in the pathogenesis of **neurofibromatosis**. Example from *Mus musculus*: database code NF1_MOUSE, 28.41 amino acids (319.59 kDa).

neurofilament a type of **intermediate filament** found in neurons.

neuroglia *an alternative name for* **glia**.

neuroglian a probable cell-adhesion molecule, with structural similarities to **neural cell-adhesion molecule** L1. It is found in neurons and glia of the developing nervous system. It has a single transmembrane domain, with extracellular immunoglobulin-like and fibronectin-type domains. Example from *Drosophila melanogaster* (presursor): database code NRGDROME, 1239 amino acids (138.28 kDa); residues 1–23 are the signal, 24–1239 neuroglian.

neurohormone any organic compound produced by neurons and released into the circulation to act as a chemical messenger; the term is sometimes extended to all **neurotransmitters** whether released or not. —**neurohormonal** *adj.*

neurohumour *or (US)* **neurohumor** a neurohormone or a neurotransmitter. —**neurohumoral** *adj.*

neurohypophysis (*pl.* **neurohypophyses**) the posterior lobe of the pituitary gland, *also called* **neural lobe** *or* **pars nervosa**. It secretes the peptide hormones oxytocin and vasopressin, and also possibly some others. *Compare* **adenohypophysis**. —**neurohypophyseal** *or* **neurohypophysial** *adj.*

neurokinin A *or* **neuromedin L** *or* **substance K** the peptide hormone

His-Lys-Thr-Asp-Ser-Phe-Val-Gly-Leu-Met

derived from **protachykinin β precursor**. It is a member of the **tachykinin** family and is a potent bronchoconstrictor. The related peptide [βAla^8]neurokinin A 4–10,

H-Asp-Ser-Phe-Val-βAla-Leu-Met-NH_2,

is a potent and selective **substance K receptor** agonist.

neurokinin B *or* **neuromedin K** a member of the **tachykinin** family that has neuroendocrine and neuroexcitatory functions, especially in the olofactory, gustatory, and visceral systems. It is a potent bronchioconstrictor. It has the sequence

Asp-Met-His-Asp-Phe-Phe-Val-Gly-Leu-Met-NH_2

database code TKNK_PIG, 10 amino acids (1.211 kDa). Neurokinin B acts through a G-protein-coupled receptor, known as NK-3, linked to the phosphatidylinositol cycle.

neurolemma *a variant spelling of* **neurilemma**.

neuroleptic any drug used to treat major psychosis, e.g. schizophrenia or mania. Such drugs include phenothiazines, e.g. **chlorpromazine**, and butyrophenones, e.g. **haloperidol**.

neurolysin EC 3.4.24.16; *other name*: neurotensin endopeptidase; an enzyme that catalyses the preferential cleavage in neurotensin of Pro^{10}-|-Tyr^{11}.

neuromedin B a decapeptide first isolated from porcine spinal cord. Its structure,

Gly-Asn-Leu-Trp-Ala-Thr-Gly-His-Phe-Met,

has close sequence homology to **bombesin**, with which it shares mitogenic and growth-promoting properties. In rat brain its concentration is highest in the olfactory bulb, but is also high in the hypothalamus, hippocampus, and spinal cord. The B in its name indicates its similarity to bombesin. Example of precursor from human (which also includes oxytocin): database code NEU1_HUMAN, 125 amino acids (12.71 kDa).

neuromedin C a neuropeptide similar in its structure,

Gly-Asn-His-Trp-Ala-Val-Gly-His-Leu-Met,

and in its actions to **neuromedin B** and **bombesin**.

neuromedin L *an alternative name for* **neurokinin A**.

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neuromedin N a hexapeptide whose C-terminal tetrapeptide is identical to that of **neurotensin**.

neuromodulator *any endogenous agent that influences the* function of a **neurotransmitter** but has no direct excitatory or inhibitory postsynaptic actions. The term usually implies long-latency and long-lasting effects (i.e. seconds to days).

neuromuscular of, pertaining to, or affecting both nervous and muscular tissue.

neuromuscular junction the place of contact between the motor end-plate of the fibre of a motor neuron and the membrane of a muscle fibre supplied by the neuron. Impulses are transmitted across the gap by diffusion of a neurotransmitter. *Compare* **synapse**.

neuron *or* **neurone** *or* **nerve cell** a cell that is specialized for the transmission of nerve impulses. Neurons are the structural and functional units of the nervous system. Each consists of an enlarged portion, the cell body or perikaryon, containing the nucleus and from which project a variable number of thread-like processes. Of these the short branched dendrites convey impulses towards the cell body, while a longer single nerve fibre, or axon, conveys impulses away from the cell body. The axon is unbranched except at the nerve ending. —**neuronal** *adj.*

neuronatin a protein that is highly expressed in neonate mammalian brain and which may be involved in terminal brain differentiation. Example from rat: database code RNU08290, 81 amino acids (9.21 kDa).

neuropeptide *(sometimes)* any peptide with neuroendocrine activity.

neuropeptide K a polypeptide hormone, DADSSIEKQVALLKALYGHGQISHKRHKTDSFVGLM–NH_2, derived from **protachykinin β precursor**. It exhibits a wide spectrum of activities overlapping those of other members of the **tachykinin** family, with which it shares the C-terminal sequence FXLM-NH_2.

neuropeptide Y *or (formerly)* **melanostatin**; *abbr.*: NPY; a 36-residue peptide neurotransmitter, structure YPSKPDNPGEDAPAEDMARYYSALRHYINLITRQRY–amide (human, porcine has Leu^{17}), found in relatively high concentrations in adrenal glands, brain, and heart. It is one of the most abundant neuropeptides. It is a potent stimuulator of feeding; leptin inhibits NPY gene expression and release. NPY also regulates secretion of **gonadotropin releasing hormone**. It shows considerable sequence homology with **peptide YY** and **pancreatic polypeptide**. The active peptide is derived from a precursor; example (precursor) from human: database code NEUY_HUMAN, 97 amino acids (10.84 kDa). [Leu^{31}, Pro^{34}]NPY is a selective agonist for a Y_1 receptor subclass. *See also* **neuropeptide-Y receptor**.

neuropeptide-Y receptor *abbr.*: NPY receptor *or* Y receptor; a membrane protein that binds **neuropeptide Y** (NPY) and mediates its intracellular effects. Effector pathways involve the inhibition of adenylate cyclase and of Ca^{2+} channels. The NPY receptors are seven-transmembrane-helix G-protein-coupled single polypeptides. Four types have been recognized that vary in their affinities for NPY analogues. Example of type 4 from human: database code NY4R_HUMAN, 375 amino acids (42.19 kDa). A fifth type, Y5, is sugggested to be the receptor by which NPY exerts its effects on feeding.

neurophysin any of a small number (usually two in any given animal species) of cystine-rich, single-chain polypeptides present in the neurohypophysis. Each binds specifically and stoichiometrically either to oxytocin or to vasopressin (or to certain of their analogues) and is released with the respective hormone. Neurophysin I binds **oxytocin** and shares a common precursor; example from *Rattus norvegicus*; database code NEU1_RAT, 125 amino acids (12.8 kDa); residues 1–19 are the signal peptide, 20–28 oxytocin, 32–125 neurophysin I. Neurophysin II binds **vasopressin** and shares a common precursor; example from *R. norvegicus*; database code NEU2_RAT, 168 amino acids (17.92 kDa); residues 1–23, signal; 24–32, Arg-vasopressin; 36–128, neurophysin II. *See also* **vasopressin-neurophysin 2-copeptin precursor**.

neurophysin II *another name for* **MSEL-neurophysin**.

neuroscience any of the sciences dealing with the nervous system; such sciences collectively.

neurosecretion **1** the process of secretion of a substance by a (specially adapted) nerve cell. **2** a product of such a secretion; a **neurocrine** (def. 2) or **neuroendocrine** (def. 2). —**neurosecretory** *adj.*

neurosome *(sometimes)* a mitochondrion of a nerve cell.

Neurospora a genus of ascomycete microfungi. The species *N. crassa* has been widely used in biochemical and genetic studies. It is commonly found as a mould on bread that has been kept for too long.

neurotensin a tridecapeptide, Glp-Leu-Tyr-Glu-Asn-Lys-Pro-Arg-Arg-Pro-Tyr-Ile-Leu-OH, found in mammalian brain and gut, especially in **N cells**, packaged within secretory vesicles. It is released from the hypothalamus into the circulation. Although initially shown to induce hypotension, it is now known to have a wide variety of pharmacological actions, including muscle contraction; however, its true physiological role remains unclear. Example (precursor) from bovine: database code NEUT_BOVIN, 169 amino acids (19.69 kDa). This precursor gives rise to neurotensin and two other derivatives, neuromedin and neuromedin N.

neurotensin endopeptidase *see* **neurolysin**.

neurotoxin any toxin that acts specifically or primarily on nervous tissue. —**neurotoxic** *adj.*

neurotransmission the transmission of nerve impulses from a neuron to another excitable cell via a neurotransmitter.

neurotransmitter any chemical substance released at the distal end of the axon of a neuron in response to the arrival of a nerve impulse that, by diffusing across a **synapse** or other junction, is capable of transmitting the impulse to another neuron, to a muscle cell, or to another excitable cell or, in the case of inhibitory neurotransmitters, of inhibiting the transmission. The neurotransmitter is stored in synaptic vesicles in the axon terminal; it is released into the synaptic cleft on arrival of the action potential and diffuses to and stimulates receptors in the membrane of the post-synaptic cell. An essential component of the mechanism is a means to inactivate the neurotransmitter, e.g. by acetylcholinesterase action on acetylcholine. Both excitatory (*see* **cholinoceptor**, **purinoceptor**, and **glutamate receptor**) and inhibitory (*see* **GABA receptor** and **glycine receptor**) neurotransmitters are known.

neurotrophic factor *see* **brain-derived neurotrophic factor**.

neurotrophin *abbr.*: NT; any of a group of growth factors, similar to **nerve growth factor** but with different tissue specificities. The first to be discovered was named neurotrophin 3, as two proteins with neurotrophic properties had already been discovered (nerve growth factor and **brain-derived neurotrophic factor**). Neurotrophins have properties similar to these latter. Neutrophins 3 to 6 have been described. Examples (precursors, human): NT3, database code NT3_HUMAN, 257 amino acids (29.32 kDa); NT4 (formerly NT5), database code NT4_HUMAN, 210 amino acids (22.40 kDa).

neurotropic having a particular affinity for, or affecting nervous tissue.

neutral **1** being neither acidic nor basic (or alkaline). **2** having no net charge or electric potential.

neutral amino acid any amino acid containing equal numbers of potentially anionic and cationic groups, especially as distinct from acidic amino acids and basic amino acids.

neutral density filter *an alternative term for* **neutral filter**.

neutral fat *see* **neutral lipid**.

neutral filter *or* **neutral density filter** *(in photography and photometry)* a filter that attenuates all frequencies of light uniformly so that the relative spectral energy distribution of the transmitted light is the same as that of the incident light.

neutrality the condition, quality, or state of being **neutral** (def. 1, 2) or intermediate.

neutralize *or* **neutralise** to render **neutral** (def. 1, 2) or ineffective; to counteract. —**neutralization** *or* **neutralisation** *n.*

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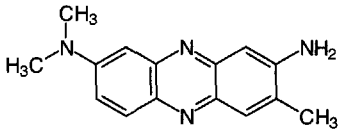
neutral lipid *an operational term for* any lipid that is soluble only in solvents of very low polarity. Neutral lipids are divided into two main groups: (1) acylglycerols (glycerides), i.e. fatty-acid esters of glycerol; and (2) waxes, i.e. fatty-acid esters of long-chain monohydroxy alcohols.

Neutral Red an indicator dye that changes colour from red to orange-brown over the pH range 6.8–8.0.



neutral solution any aqueous solution in which the activities of the hydrogen and hydroxide ions are equal. Such a solution in which water is the solé solvent has a pH of 7.00 at 25° C.

neutron *symbol*: n; an elementary particle of zero charge; nucleon number 1; rest mass 1.6749×10^{-27} kg (1.0086 Da); spin ½. Neutrons are present in the nuclei of all atoms (except the hydrogen atom), where they are stable; when free, a neutron has a mean life of 932 s, decaying to a proton and an electron.

neutron activation analysis *an alternative name for* **radioactivation analysis**.

neutron diffraction a technique that is similar in principle to **X-ray diffraction** by a crystal, and is applicable particularly to biopolymers and particulate structures. Because hydrogen atoms make a much more substantial contribution to the scattering of neutrons than to X-ray scattering the technique is useful for refining partially determined structures obtained by the use of X-rays. In rare cases it has been used for determination of absolute configuration.

neutron flux (density) the number of free neutrons passing through unit volume multiplied by their mean velocity.

neutron number *symbol*: N; a dimensionless physical quantity, having an integral value for any given nuclide, equal to the number of neutrons contained in the nucleus of an atom of the nuclide. Hence, it is equal to the arithmetical difference between the **nucleon number**, A, of the nuclide and the **proton number**, Z, of the relevant chemical element; i.e. $N = A - Z$.

neutron scattering *see* **small-angle scattering**.

neutrophil *or* **neutrophil leukocyte** *or* **neutrophilic leukocyte** the most numerous **polymorphonuclear leukocyte** found in the blood; a phagocytic cell of the myeloid series that is distinguished by the presence of cytoplasmic azurophil granules and other granules that take up neither acidic nor basic dyes. It plays a major role in the inflammatory response, undergoing chemotaxis towards sites of infection or wounding.

Newman projection a two-dimensional representation of a molecule in which the atoms are arranged as they would be seen if the molecule were viewed from one end along the carbon–carbon bond nearest to the observer. *See also* **conformation**.

newton *symbol*: N; the SI derived unit of force, defined as the force required to give a mass of one kilogram an acceleration of one metre per second per second; i.e.

$$1\ \mathrm{N} = 1\ \mathrm{kg\ m\ s^{-2}} = 1\ \mathrm{J\ m^{-1}}\ (= 10^5\ \text{dynes}).$$

Newton, (Sir) Isaac (1642–1727), English astronomer, mathematician, philosopher, and physicist. —**Newtonian** *adj.*

Newtonian flow the type of flow displayed by a **Newtonian fluid**.

Newtonian fluid any fluid whose (coefficient of) viscosity is independent of flow rate, conforming to **Newton's law of viscosity**.

Newton's law of viscosity a law that describes the flow of almost all fluids of low relative molecular mass and also that of some solutions of macromolecules. A fluid moving between two parallel plates, in the x direction with a velocity v, is thought of as a number of infinitesimal layers, each of which slides along the adjacent one, the frictional resistance between adjacent layers generating an orthogonal velocity gradient, in the y direction. The frictional force, f, between the fluid layers is then proportional to the area, A, of the layers and to the velocity gradient between them, such that:

$$f = \eta A(\mathrm{d}v/\mathrm{d}y),$$

where the constant η is known as the **coefficient of viscosity** (or **viscosity** for short) at the temperature of measurement; its reciprocal, $1/\eta$, is the **fluidity**.

new yellow enzyme *an obsolete name for* the enzyme D-amino-acid oxidase (EC 1.4.3.3), a yellow flavoprotein (FAD) with wide specificity for D-amino acids and acting also on glycine. It was so-named to distinguish it from **old yellow enzyme**. *See* **amino-acid oxidase**.

New Zealand obese mouse *abbr.*: NZO mouse; one of a number of strains of genetically obese mice that are used in metabolic and endocrine research. The obesity is moderate in character and there is an associated hyperinsulinemia and hyperglycemia.

nexin a protein found in the **axoneme** of eukaryotic cilia and flagella. It forms interconnections between the microtubule outer doublets that surround the inner central pair of microtubules. *See also* **glial-derived nexin**.

nexin 1 *other names*: protease nexin I (*abbr.*: PN-I); a glycoprotein that promotes neurite extension and is an extracellular **serpin**-like serine protease inhibitor. Example, residues 20–398 of the human glial derived nexin precursor (GDN): database code GDN_HUMAN, 398 amino acids (43.95 kDa).

nexin 2 the secreted isoform of the Alzheimer's amyloid β-protein precursor (*see* **β-amyloid peptide**). *See also* **Alzheimer's disease**.

nexus *(in cytology) an alternative name for* **gap junction**.

NF-1 *see* **CTF, neurofibromin**.

NF2 *abbr. for* neurofibromatosis type-2 tumour suppressor; *see* **merlin**.

NF-κB a transcription factor for eukaryotic RNA polymerase II promoters. In humans the active protein is a heterodimer of two DNA-binding subunits (p50) which belong to the same family as the **dorsal protein**. It is found in cytoplasm as an inactive complex with an inhibitory subunit, IκB; activation of NF-κB involves its release from its inhibitory subunit. A 105 kDa protein is the precursor of the p50 subunits. These bind to the **kappa-B** consensus sequence, GGRNNYYCC, e.g. GGGGACTTTCC in mouse and human. Example from *Gallus gallus*: database code KBF1_CHICK, 984 amino acids (108.17 kDa).

NF-E1 *see* **GATA-1**.

ng *symbol for* nanogram.

NGF *abbr. for* nerve growth factor.

L-NHA *abbr. for* N^{G}-hydroxy-L-arginine.

Ni *symbol for* nickel.

niacin *an alternative name for* **nicotinic acid**.

niacinamide *an alternative name for* **nicotinamide**.

NICE element *abbr. for* nodule infected cell expression element, a name given to an AT-rich element in *Sesbania rostrata* leghemoglobin glb3.

NICER elements *a name suggested for* a family of genes that are nerve growth factor-inducible, cyclic AMP-extinguishable, and retrovirus-like, hence the acronym.

nick 1 an interruption in the covalent continuity of one strand of a double-stranded nucleic-acid molecule. 2 to produce a nick in a nucleic-acid molecule. *See also* **nick translation**.

nickase an endodeoxyribonuclease present in phage-infected *Escherichia coli* cells that gives rise to single-strand breaks (nicks) in duplex DNA.

nickel *symbol*: Ni; it is a ferromagnetic, metallic transition element of group 10 of the IUPAC **periodic table**; atomic number 28; relative atomic mass 58.69. It consists of a mixture of five stable nuclides of which the two most abundant are those of mass numbers 58 and 60; its commonest valence is II. Nickel's abundance in the Earth's crust is 0.018% and it is an essential

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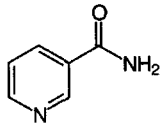
trace element for living organisms. Several artificial radionuclides of nickel are known, including nickel-56 (γ-emitter; half-life 6.1 days) and nickel-63 (emits β^- radiation, 0.066 MeV; half-life 100 years).

nicking–closing enzyme *or* **nicking-and-closing enzyme** *see* type I **DNA topoisomerase**.

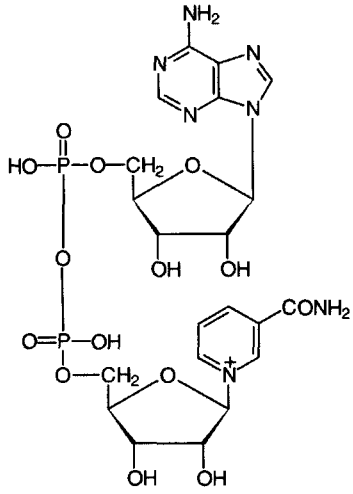
nick translation a procedure for preparing radioactively labelled DNA, especially for use as probes in hybridization experiments. Single-stranded nicks are introduced into unlabelled DNA, usually by limited treatment with deoxyribonuclease I, exposing 3′-hydroxyl termini. *Escherichia coli* DNA polymerase I (at low temperature, ≈15 °C) is then used successively to incorporate radioactive nucleotides (present as dNTPs in the reaction mixture) to form a new, radioactively labelled polynucleotide strand while the 5′→3′ exonuclease activity of the polymerase concomitantly hydrolyses the 5′ termini ahead of the growing strand, liberating 5′-mononucleotides. The reaction thus progressively replaces nucleotide residues by their labelled counterparts in a DNA duplex, which is otherwise unchanged except for the translation of the nick, i.e. its progressive displacement towards the 3′ end of the strand. (The word 'translation' in the name may be misleading as the function involved is replication.)

Nicol prism an optical device constructed of two prisms of calcite cemented together with Canada balsam, used for producing plane polarized light and/or determining its orientation. It has now largely been superseded by Polaroid filters, etc. [After William Nicol (1768–1851), British physicist.]

nicotinamide *the recommended trivial name for* pyridine-3-carboxamide, the amide of **nicotinic acid**; *also called* **niacinamide**. It is a member of the B complex of vitamins, and is nutritionally equivalent to nicotinic acid. It occurs widely in living organisms, usually in combined form.

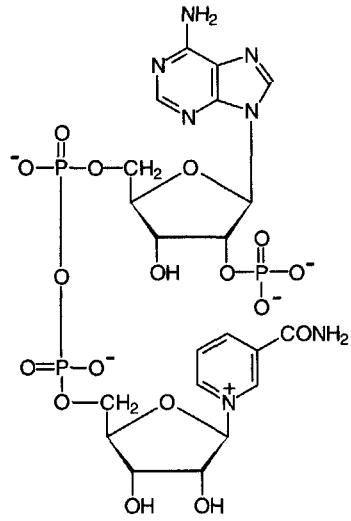


nicotinamide-adenine dinucleotide *abbr.*: NAD^+ *or* NAD; if the oxidation state is not to be specified; nicotinamide(1)-β-D-riboside(5′)diphospho(5′)adenosine; an atypical dinucleotide containing a phosphoric anhydride linkage in place of the usual phosphodiester linkage between the component mononucleotide units, i.e. between nicotinamide mononucleotide and adenylic acid. It is the specific coenzyme in



numerous oxidoreductase enzyme reactions, although in a number it functions interchangeably with **nicotinamide-adenine dinucleotide phosphate**. In these reactions it stereospecifically accepts a hydrogen atom at position 4 of the pyridine ring, plus an electron, to form **nicotinamide-adenine dinucleotide (reduced)**. It acts also as a donor in the ADP-ribosylation of some eukaryotic and prokaryotic proteins. The α anomer is inactive as a coenzyme. *Former names*: codehydrogenase I; coenzyme I (Co I); cozymase; diphosphopyridine nucleotide (DPN). *See also* **nicotinamide-adenine dinucleotide (reduced)**.

nicotinamide-adenine dinucleotide phosphate *abbr.*: $NADP^+$; nicotinamide(1)-β-D-riboside(5′)diphospho(5′)adenosine 2′-phosphate; a coenzyme with a structure and coenzymic mechanism related to those of **nicotinamide-adenine dinucleotide**, although it functions as the sole coenzyme for fewer oxidoreductases and tends to be involved more in synthetic than in energy-yielding reactions. *Former names*: codehydrogenase II; coenzyme II (Co II); phosphocozymase; triphosphopyridine nucleotide (TPN). *See also* **nicotinamide-adenine dinucleotide phosphate (reduced)**.



nicotinamide-adenine dinucleotide phosphate (reduced) *abbr.*: NADPH; 3-aminocarbonyl-1,4-dihydropyridine(1)-β-D-riboside (5′)diphospho(5′)adenosine 2′-phosphate; the reduced form of the coenzyme **nictoinamide-adenine dinucleotide phosphate**. As in **nicotinamide-adenine dinucleotide (reduced)** the carbon atom at position 4 of the 1,4-dihydropyridine ring is prochiral. *See also* **NAD(P)$^+$ stereospecificity**. *Former names*: reduced codehydrogenase II; reduced coenzyme II (Co IIH_2); reduced phosphocozymase; reduced triphosphopyridine nucleotide (TPNH).

nicotinamide-adenine dinucleotide (reduced) *abbr.*: NADH; 3-aminocarbonyl-1,4-dihydropyridine(1)-β-D-riboside(5′)diphospho(5′)adenosine; the reduced form of the coenzyme **nicotinamide-adenine dinucleotide**. The carbon atom at position 4 of the dihydropyridine ring is prochiral; removal of one of the two hydrogen atoms from position 4 (or introduction of a hydrogen atom at this position into the oxidized form) through the agency of an NAD-linked oxidoreductase is stereospecific, the two hydrogen atoms being designated *pro-R* (or H_A) or *pro-S* (or H_B), and the two corresponding aspects of the (dihydro)pyridine ring frequently being known as the *A* face and the *B* face. The α anomer is inactive as a coenzyme. *Former names*: reduced codehydrogenase I; reduced coenzyme I (Co IH_2); reduced cozymase; reduced diphosphopyridine nucleotide (DPNH). *See also* **NAD(P)$^+$ stereospecificity**.

nicotinamide mononucleotide *symbol*: NMN; nicotin-

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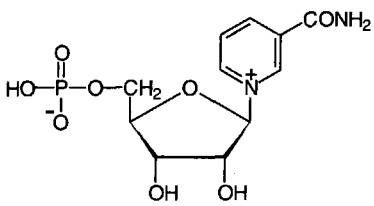
amide(1)-β-D-riboside 5′-phosphate; the mononucleotide produced when **nicotinamide-adenine dinucleotide** acts as a donor of an adenylyl group in the activation of DNA ligase.



nicotinamide mononucleotide

nicotinamide nucleotide any nucleotide that contains combined nicotinamide, e.g. nicotinamide-adenine dinucleotide (reduced), nicotinamide-adenine dinucleotide phosphate (reduced).

nicotinamide–nucleotide adenylyltransferase EC 2.7.7.1; *other name*: NAD^+ pyrophosphorylase; an enzyme that catalyses the formation of NAD^+ from ATP and nicotinamide ribonucleotide with release of pyrophosphate and NAD^+. *See also* **NAD^+ synthase**, **NAD^+ synthase (glutamine-hydrolysing)**.

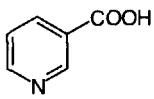
nicotinate pyridine 3-carboxylate; the anion derived from **nicotinic acid**.

nicotinate mononucleotide 3-carboxylatopyridine(1)-β-D-riboside 5′-phosphate; an intermediate in the biosynthesis of nicotinamide-adenine dinucleotide. It reacts with ATP to form desamido-NAD, which is subsequently converted to NAD by a glutamine-dependent amidation of the carboxyl group.

nicotine (*S*)(−)-3-(1-methyl-2-pyrrolidinyl)pyridine; the principal example of a number of related very poisonous and addictive alkaloids extractable from the dried leaves of various species of tobacco, especially *Nicotiana tabacum*. It is an agonist of the nicotinic class of **cholinoceptors**. —**nicotinic** *adj.*

nicotinic acetylcholine receptor *see* **cholinoceptor**.

nicotinic acid *abbr.*: NA; *the recommended trivial name for* pyridine 3-carboxylic acid, *also known as* niacin. It is a member of the B complex of vitamins, nutritionally equivalent to **nicotinamide**. At physiological pH values it exists virtually exclusively as the nicotinate anion.

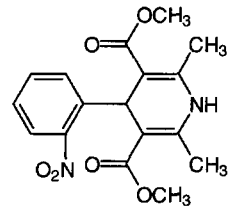


nidogen *or* **entactin** a sulfated glycoprotein that is widely distributed in basement membranes and tightly associated with **laminin**. Example (precursor) from human: database code NIDO_HUMAN, 1247 amino acids (136.34 kDa).

Niemann–Pick disease *an alternative name for* **sphingomyelin lipidosis**. [After Albert Niemann (1880–1920), German physician.]

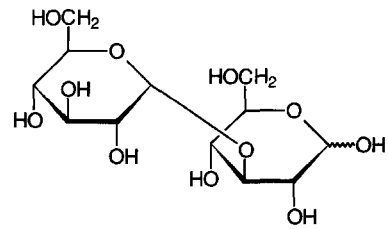
nif the symbol for any gene controlling bacterial nitrogen fixation; individual genes are distinguished by suffixed capital letters, e.g. *nifB*, *nifQ*. In *Klebsiella pneumoniae* the *nif* cluster has at least 18 genes, arranged in seven distinct operons with no other interspersed genes; the total length of the *nif* region is ≈24 kb. The two polypeptide subunits of component I of **nitrogenase** and the polypeptide subunit of component II are each controlled by a single *nif* gene; the production and insertion of iron–molybdenum cofactor (FeMo-co) into component I appears to require three to six genes; the production of mature component II is controlled by two to four genes; two electron-transporting proteins are coded for by one gene each; and three or more genes are concerned with regulating expression of others.

nifedipine 1,4-dihydro-2,6-dimethyl-4-(2-nitrophenyl)-3,5-pyridinedicarboxylic acid dimethyl ester; one of the dihydropyridine calcium antagonists. It is a calcium channel blocking agent inhibiting the cellular influx of calcium associated with the plateau phase of the action potential. It acts as a vasodilator, reducing blood pressure and increasing coronary blood flow.



nigericin a 725 Da, open-chain macrotetrolide-like antibiotic, with many chiral centres, isolated from *Streptomyces hygroscopicus*. It forms stable complexes with monovalent cations, especially with K^+; these complexes are soluble in organic solvents, and thus nigericin can act as an ionophore for monovalent cations. It has some structural resemblance to **monensin**.

nigerose the disaccharide 3-*O*-α-D-glucopyranosyl-D-glucose.



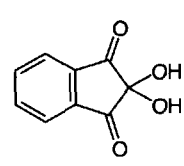
night blindness *or* **nyctalopia** the inability to see in dim light or at night. It is due to degeneration of the **rod cells** in the retina of the eye, which primarily mediate vision in dim light.

NIH *abbr. for* National Institutes of Health (of the USA).

NIH shift *or* **hydroxylation-induced migration** an intramolecular migration that often occurs in the hydroxylation reactions of alkylaromatic compounds catalysed by certain mono- or dioxygenases, whereby a hydrogen atom or a substituent atom or group at the position of hydroxylation moves to an adjacent carbon atom in the aromatic ring. For example, in the hydroxylation of phenylalanine to tyrosine, catalysed by phenylalanine 4-monooxygenase (EC 1.14.16.1), the hydrogen atom at C-4 in the ring can be shown by tritium labelling to migrate to C-3. [After NIH, i.e. National Institutes of Health, where the discoverers were based.]

NIMR *abbr. for* National Institute for Medical Research (of the UK).

ninhydrin *the trivial name of* triketohydrindene hydrate; 2,2-dihydroxy-1,3-indanedione; a pale-yellow crystalline substance, useful as a sensitive chromogenic reagent for the detection and quantification of compounds containing free amino or imino groups. The common amino acids (and the free amino groups of peptides and proteins, and various other amino compounds) give a red, violet, or blue coloration, the shade depending somewhat on conditions, whereas the imino acids proline and



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hydroxyproline give a yellow colour. The partially reduced ninhydrin derivative, hydrindantin, is often added to the reagent solution, as it reacts with free ammonia that is formed as a side product, and in combination with ninhydrin forms the coloured product, thus enhancing the sensitivity of the reaction.

Nir *symbol for* the ribonucleoside ribosylnicotinamide.

Nirenberg, Marshall Warren (1927–), US biochemist and molecular biologist; Nobel Laureate in Physiology or Medicine (1968) jointly with R. W. Holley and H. G. Khorana 'for their interpretation of the genetic code and its function in protein synthesis'.

Nissl substance *a collective term for* the dense regions of granular endoplasmic reticulum and free polysomes observable by microscopy within the cytoplasm of the cell body of vertebrate neurons. [After Franz Nissl (1860–1919), German neuropathologist, who first observed it.]

nitrate **1** the NO_3^- ion, derived from nitric acid. **2** any salt or ester of nitric acid.

nitrate assimilation *an alternative term for* assimilatory nitrate reduction; *see* **nitrate reduction**.

nitrate dissimilation *an alternative term for* dissimilatory nitrate reduction; *see* **nitrate reduction**.

nitrate reductase **1** any of the three enzymes designated **nitrate reductase (NADH)** (EC 1.6.6.1), **nitrate reductase (NAD(P)H)** (EC 1.6.6.2), or **nitrate reductase (NADPH)** (EC 1.6.6.3) that reduce nitrate to nitrite coupled to the oxidation of the coenzymes indicated. They are of widespread occurrence in plants and microorganisms, where they participate in assimilatory nitrate reduction. All are flavoproteins, usually containing one atom of molybdenum per molecule. Example from *Arabidopsis thaliana*: database code NIA1_ARATH, 917 amino acids (103.12 kDa). **2** the microbial enzyme, designated nitrate reductase (EC 1.7.99.4), that reduces nitrate to nitrite coupled to the oxidation of various electron donors in dissimilatory nitrate reduction. Example from *Bacillus subtilis*: database code NARG_BACSU, 1228 amino acids (139.08 kDa). **3** the microbial enzyme, designated **nitrate reductase (cytochrome)** (EC 1.9.6.1), that reduces nitrate to nitrite coupled to the oxidation of a ferrocytochrome to the corresponding ferricytochrome. *See also* **nitrate reduction**.

nitrate reduction any reaction or sequence of reactions in which nitrate ion is converted to other less highly oxidized inorganic nitrogenous substances, e.g. to nitrite ion, nitrous oxide, dinitrogen, ammonium ion, or amino acids. In enzymology the term is restricted to the enzymic reduction of nitrate ion to nitrite ion, catalysed by a **nitrate reductase** enzyme. In biology, nitrate reduction is of two types, distinguishable by the purposes served and by the enzymes involved. **Assimilatory nitrate reduction** is the process occurring in higher plants, algae, and fungi, in which nitrogen from nitrate is converted into organic nitrogen-containing compounds, via the probable reaction sequence: nitrate → nitrite → [hyponitrite] → hydroxylamine → ammonium → amide group of glutamine → amino acids, etc. **Dissimilatory nitrate reduction** or **nitrate respiration** is the process occurring in some microorganisms under anaerobic conditions in which nitrate functions as a terminal electron acceptor in respiratory metabolism. The nitrogen may either be converted to ammonium (which is not assimilated), a process designated **ammonification of nitrate**, or be converted to various gaseous compounds such as nitric oxide, nitrous oxide, and/or dinitrogen, a process designated **denitrification**. *Compare* **nitrification**.

nitrene the chemical entity NH or any of its substitution derivatives. It contains an electrically neutral mono-coordinate nitrogen atom with four nonbonding electrons; two of these electrons are paired while the other two have spins that may be either antiparallel (singlet state) or parallel (triplet state). *Other names*: azacarbene; azene; imene; imine radical.

nitric oxide nitrogen monoxide; NO; a colourless gas, only slightly soluble in water, that reacts readily with O_2 to form nitrogen dioxide, NO_2; it can form the stable cation NO^+. It has been found to account for the action of endothelium-derived relaxing factor (EDRF). Nitric oxide is a biogenic messenger with potent actions causing *inter alia* vasodilation, inhibition of platelet aggregation, and reduction of endothelium adhesion; it also has anticoagulant and fibrinolytic actions. It is formed biosynthetically from L-arginine by **nitric-oxide synthase** in most mammalian tissues in varying amounts, including vascular endothelial cells, the central and peripheral nervous system, immune cells, lung, or liver. It activates guanylate cyclase, producing cyclic GMP. It is oxidized to nitrite, then to nitrate, which is present in the blood.

nitric-oxide synthase EC 1.14.13.39; *abbr.*: NOS; *systematic name*: L-arginine,NADPH:oxygen oxidoreductase (nitric-oxide-forming). An enzyme that catalyses a reaction between L-arginine, NADPH, and O_2 in which citrulline, $NADP^+$, and nitric oxide are formed; heme, FAD, FMN, and tetrahydrobiopterin are required as cofactors; the heme centre has the spectral properties of a cytochrome P450; N^{ω}-hydroxy-L-arginine is an intermediate, and acts as a substrate for the enzyme. Three isoforms are known: **nNOS**, originally expressed in neuronal tissues, and **eNOS**, first identified in vascular endothelial cells, are both expressed constitutively and are Ca^{2+}-dependent; **iNOS**, first identified as an enzyme inducible in macrophages and liver cells, is not Ca^{2+}-dependent, but binds calmodulin with extremely high efficiency. All have consensus sequences for the binding of NADPH, FAD, FMN, and calmodulin, and a phosphorylation site for cyclic-AMP-dependent protein kinase A; eNOS has an N-terminal consensus sequence for myristoylation. Inhibitors include L-N^5-(1-iminoethyl)ornithine, N^G-monomethyl-L-arginine, N^G-nitro-L-arginine. Example, from human endothelial cells: database code NOS3_HUMAN, 1202 amino acids (133.15 kDa).

nitrification the process by which certain soil bacteria (nitrifying bacteria) oxidize ammonium ions in decomposing organic material into nitrate ions. *Nitrosomonas* spp. first convert ammonium to nitrite, and *Nitrobacter* spp. then oxidize nitrite to nitrate. The process is important because most higher plants can assimilate nitrate much more readily than they can ammonium. *Compare* **denitrification**.

nitrify **1** (of nitrifying bacteria) to oxidize ammonium to nitrate. **2** to treat (soil) with nitrates. —**nitrified** *or* **nitrifying** *adj.*

nitrifying bacteria obligately aerobic bacteria that are capable of oxidizing ammonia to nitrite, and nitrite to nitrate. *See* **nitrification**. *Compare* **denitrifying bacteria**.

nitrite **1** the NO_2^- ion, derived from nitrous acid. **2** any salt or ester of nitrous acid.

nitrite reductase **1** the enzyme designated **nitrite reductase (NAD(P)H)** (EC 1.6.6.4) that reduces nitrite to ammonium coupled to the oxidation of either NADH or NADPH. It is a flavin-dependent enzyme that also contains **siroheme**; it participates in assimilatory **nitrate reduction** in higher plants, algae, fungi and bacteria. Example from *Bacillus subtilis*: database code NASD_BACSU, 805 amino acids (88.43 kDa). **2** the enzyme designated **nitrite reductase (cytochrome)** (EC 1.7.2.1) that reduces nitrite to nitric oxide coupled to the oxidation of ferrocytochrome *c* to ferricytochrome *c*. It is a cuproprotein and participates in denitrification processes in some microorganisms. **3** the enzyme designated **ferredoxin–nitrite reductase** (EC 1.7.7.1) that reduces nitrite to ammonium coupled to the oxidation of reduced ferredoxin; the enzyme in spinach leaves contains one molecule of siroheme and one iron–sulfur (Fe_2S_2) cluster per molecule. It participates in assimilatory nitrate reduction, the reduced ferredoxin being derived from the light reactions of photosynthesis. Example from *Zea mays*: database code NIR_MAIZE, 569 amino acids (63.34 kDa). **4** the microbial enzyme, designated nitrite reductase (EC 1.7.99.3), that reduces nitrite to nitric oxide coupled to the oxidation of various electron donors in dissimilatory nitrate reduction; the enzymes from *Achromobacter cycloclastes* and *Pseudomonas*

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denitrificans contain copper: database code NIR_ACHCY, 340 amino acids (37.01 kDa).

nitro the chemical group $-NO_2$ in a molecule of an organic compound.

nitro+ *prefix (in chemical nomenclature)* **1** indicating the presence of a **nitro** group in an organic compound. **2** *(in chemical technology)* indicating that a chemical compound is a nitrate ester.

Nitroblue Tetrazolium *see* **Nitrotetrazolium Blue**.

nitrogen **1** *symbol*: N; a nonmetallic element of group 15 of the IUPAC **periodic table**; atomic number 7; relative atomic mass 14.0067. There are two natural stable nuclides of relative masses 14 (99.635 atom percent) and 15 (*see* **nitrogen-15**); its commonest valences are III and IV. Nitrogen occurs naturally in the form of diatomic molecules of the gas dinitrogen (see below) and in combined form in numberless organic molecules in all forms of life. *See also* **nitrogen-13**. **2 dinitrogen** *or* **molecular nitrogen** *symbol*: N_2; a diatomic nonflammable gas. It constitutes 75.5% by mass, or 75.06% by volume, of the Earth's atmosphere, and undergoes exchange with organically combined nitrogen via the processes of the **nitrogen cycle**. Liquid nitrogen, b.p. 77.36 K, is commonly used as a coolant or freezing agent.

nitrogen-13 the artificial radioactive nitrogen nuclide $^{13}_{7}N$. It emits a positron (β^+-particle) (1.19 MeV max.) and no gamma radiation; it has a half-life of 9.96 min.

nitrogen-15 heavy nitrogen; the stable, naturally occurring nitrogen nuclide $^{15}_{7}N$; relative abundance in nitrogen 0.365 atom percent. It is extensively used as a tracer in studies of nitrogen metabolism and in **nuclear magnetic resonance**.

nitrogenase an enzyme complex that catalyses the ATP-dependent process of biological fixation of atmospheric nitrogen, summarized by the equation:

$$N_2 + 8H^+ + 6e^- \rightarrow 2NH_4^+.$$

The electrons may be donated by either 3 reduced ferredoxin (this enzyme is EC 1.18.6.1) or 6 reduced flavodoxin (this enzyme is EC 1.19.6.1), depending on the bacterial species, the following summary being based on the systems utilizing ferredoxin. Nitrogenase consists of two oxygen-sensitive components, known as **component I** (*other names*: dinitrogenase; MoFe protein; molybdoferredoxin) and **component II** (*other names*: dinitrogenase reductase; Fe protein; azoferredoxin), in the molar ratio 1:2. Component I is a tetramer made up of two different polypeptide chains of about 50 and 60 kDa, each present twice; the tetramer also contains two Mo atoms, around 30 Fe atoms and about 30 acid-labile sulfide groups, some of the Mo, Fe, and S being present as iron-molybdenum cofactor (*abbr.*: FeMo-co). The extremely oxygen-sensitive component II is a dimer of identical, ≈30 kDa, polypeptide chains; each dimer contains four Fe atoms and four acid-labile sulfide groups. Electrons from a donor, which may be NADPH, are transferred, via reduced ferredoxin, to component II; then, in the presence of Mg^{2+} and ATP, they are passed to component I where Mo(VI) atoms are reversibly reduced to Mo(IV), the electrons ultimately being used in three two-electron steps to reduce dinitrogen to ammonium with concomitant hydrolysis of 4–5 molecules of ATP per two electrons transferred. Nitrogenase also catalyses ATP-dependent partial reductions of some other small-molecule substances that are isoelectronic with dinitrogen, e.g. acetylene, azide, cyanide, and nitrous oxide. The biosynthesis of nitrogenase is controlled by the ***nif*** cluster of genes. Example from *Klebsiella pneumoniae*: the subunits are named from the *nif* genes; the enzyme consists of (i) a Mo–Fe protein (component I) with two α (NifD) and two β (NifK) subunits with 30–32 Fe, 2 Mo, and S (inorganic); database codes NIFD_KLEPN, 483 amino acids (54.10 kDa) and NIFK_KLEPN, 520 amino acids (58.34 kDa); (ii) an Fe protein (NifH, component II, four motifs) homodimer (one 4Fe–4S cluster per dimer); database code NIFH_KLEPN, 292 amino acids (31.74 kDa). Associated proteins are NifE (database code NIFE_KLEPN, 457 amino acids (50.10 kDa)) and NifN (database code NIFN_KLEPN, 461 amino acids (50.51 kDa)) – these are involved in FeMo-co biosynthesis; NifM (database code NIFM_KLEPN, 266 amino acids (30.58 kDa)) is involved in synthesis/activation of NifH.

nitrogenase reductase *another name for* dinitrogenase reductase; i.e. component II of **nitrogenase**.

nitrogen balance **1** *(in physiology)* the **balance** (def. 1) of the nitrogen content of the nutrients and the excretory products of an organism. **2** *(in agriculture)* the net loss or gain of the nitrogen content of soil that results from removal of nitrogen by cropping, leaching, etc. and addition of nitrogen by nitrogen fixation or addition of nitrogenous fertilizers.

nitrogen base *an alternative term for* **nitrogenous base**.

nitrogen cavitation *an alternative name for* **pressure homogenization**.

nitrogen cycle the complex series of chemical processes by which various inorganic and organic nitrogenous compounds are interconverted and maintained in equilbrium in the biosphere. It consists essentially of **nitrogen fixation**, **nitrification**, and **denitrification**, together with assimilatory and dissimilatory **nitrate reduction** and the interconversion of nitrogenous organic matter and ammonium. Individual reactions in the series may be effected by microorganisms, plants, or animals, with contributions from nonbiological processes such as manufacture of nitrogenous fertilizers, the action of lightning, and emission of combustion products.

nitrogen equilibrium the state of **nitrogen balance** (def. 1) when nitrogen intake equals nitrogen excretion.

nitrogen fixation any biological or nonbiological process that converts atmospheric dinitrogen into inorganic nitrogenous compounds; the meaning is often extended to include the biological assimilation of ammonium so produced. Biological nitrogen fixation occurs by the action of the enzyme **nitrogenase**, found in certain species of bacteria – the nitrogen-fixing bacteria.

nitrogen mustard any of a group of bis(2-chloroalkyl)amines, as typified by the volatile base bis(2-chloroethyl)ethylamine, $CH_3–CH_2–N(CH_2–CH_2Cl)_2$, a nitrogen-containing analogue of **mustard gas**. They are potent alkylating agents, vesicants, and mutagens. They cross-link DNA chains and have been used as immunosuppressive and antineoplastic agents.

nitrogenous **1** of or relating to **nitrogen**. **2** of or relating to any substance containing nitrogen in combined form.

nitrogenous base *or* **nitrogen base** *a generic term for* ammonia or any trivalent compound of nitrogen that can be regarded as a derivative of ammonia; all except quaternary ammonium compounds are weakly basic in character. In biochemistry, the term usually denotes any purine or pyrimidine; now generally shortened to base.

nitrogen regulatory protein *abbr.*: NR protein; any of several proteins of a regulatory system for transcriptional control of the glutamine-ammonia ligase, and for its regulation at the structural level. Transcriptional regulation is mediated by the proteins NR_I, that when phosphorylated acts as a transcriptional activator of the gene *glnA* and NR_{II}, a kinase that converts NR_I to NR_I-P, the phosphorylated, active form. Another protein P_{II}, prevents this phosphorylation, thereby preventing transcriptional activation. P_{II} can be uridylylated at Tyr^{51} to P_{II}-UMP by a **uridylyl transferase**, and then does not inhibit NR_I phosphorylation, so activating transcription. This occurs when the level of nitrogen is low. Regulation at the structural level of glutamate–ammonia ligase involves adenylylation by adenylyl transferase, which inactivates it. Adenylyl transferase is activated by P_{II}. In the presence of P_{II}-UMP, adenylyl transferase is inactivated, and glutamate–ammonia ligase reverts to a non-adenylylated, active form. Uridylylation of P_{II} thus results in activation of transcription of glutamate–ammonia ligase, and its activation at the structural level. Example of P_{II} from *Escherichia coli*, a homotrimer: database code GLNB_ECOLI, 112 amino acids (12.41 kDa).

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nitroglycerin 1,2,3-propanetriol trinitrate; a compound that is used industrially in the manufacture of dynamite, and pharmacologically as an antianginal and coronary vasodilator. Its action in the latter case results from its conversion to **nitric oxide**.

nitrophenyl a group that is linked to a variety of compounds to form artificial substrates for enzymes. The nitrophenol released by the enzyme action can then be measured spectrophotometrically at 400 nm (4-nitrophenol) or 420 nm (2-nitrophenol) to follow the enzyme reaction, the esterified form having a maximal absorption at a much lower wavelength. Typical substrates are 4-nitrophenylacetate (for carboxylesterase, lipase), 4-nitrophenyl-*N*-acetylgalactosaminide (galactosaminidase), 4-nitrophenyl-*N*-acetylglucosaminide (glucosaminidase), and 2-nitrophenylbutyrate (cholinesterase).

nitroprusside test a test for free thiol groups based on the red coloration given on reaction of thiol-containing compounds with ammoniacal sodium nitroprusside, sodium nitrosopentacyanoferrate(III), $Na_2[Fe(CN)_5NO]$. Nitroprusside also reacts with ketones and is used in tests for ketone bodies in urine. The proprietary Acetest tablets contain a mixture of glycine, sodium nitroprusside, disodium phosphate, and lactose. In the presence of glycine, acetoacetate or acetone forms a blue–purple colour. A positive reaction indicates the presence of ≥5 mg dL^{-1} and 10 mg dL^{-1} for urine and blood respectively.

nitros+ *a variant form of* **nitroso+** (before a vowel).

***N*-nitrosamide** any organic compound in which a **nitroso** group is attached to an amide nitrogen, e.g. *N*-methyl-*N*-nitrosourea. *See also* ***N*-nitrosamine**.

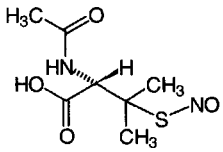
***N*-nitrosamidine** any organic compound in which a **nitroso** group is attached to an amidine nitrogen, e.g. *N*-methyl-*N'*-nitro-*N*-nitrosoguanidine. *See also* ***N*-nitrosamine**.

***N*-nitrosamine** any organic compound of general formula R_1R_2NNO. They are stable compounds formed by the action of nitrous acid on secondary amines with concurrent monodealkylation, and also on some tertiary amines. Most nitrosamines are strongly carcinogenic and their metabolites are strong mutagens. ***N*-nitrosamides** and ***N*-nitrosamidines** are unstable nitroso compounds that decompose in neutral or alkaline conditions to produce powerful alkylating agents. They are widely used as experimental mutagens. They are carcinogenic in any tissue with which they come into contact.

nitroso the chemical group –NO in a chemical compound.

nitroso+ *or (before a vowel)* **nitros+** *prefix (in chemical nomenclature)* indicating the presence of a **nitroso** group in a chemical compound; in *C*-nitroso compounds the –NO is attached to carbon (e.g. nitrosobenzene) and in *N*-nitroso compounds it is attached to nitrogen.

***S*-nitroso-*N*-acetylpenicillamine** *abbr.*: SNAP; an *S*-nitrosothiol reagent that stimulates guanylate cyclase and mimics the action of nitric oxide.



S-nitroso-*N*-acetyl-D-penicillamine

Nitrotetrazolium Blue *or* **Nitroblue Tetrazolium** a dye very similar in structure to Tetrazolium Blue (*see* **tetrazolium salt**), differing only in that each of the two tetrazolium groups has a nitrophenyl group in place of a phenyl group.

nitrous acid the very unstable monobasic acid HNO_2. It reacts with amines, including purine and pyrimidine amines, to form the corresponding hydroxy compounds, and is thus mutagenic.

nitroxide the divalent group =N–O˙ in a molecule of an organic compound. It has an unpaired electron, and is useful in spin-labelling, its derivatives being stable free radicals.

NK cell *abbr. for* natural killer cell; a large granular lymphocyte that recognizes structures on the surface of virally infected cells, which it kills, probably through the mediation of a **perforin**.

NKSF *abbr. for* NK stimulating factor. *See* **interleukin 12**.

Nle *symbol for* the α-amino acid norleucine (now known as 2-aminohexanoic acid, *symbol*: Ahx).

NLS *abbr. for* nuclear localization signal.

nm *symbol for* nanometre.

nM *or* **nM** *symbol for* nanomolar.

NMDA *abbr. for N*-methyl-D-aspartate.

NMDA receptor *see* **glutamate receptor**.

NMN *abbr. for* nicotinamide mononucleotide.

nmol *symbol for* nanomole.

NMP *abbr. for* any (unknown or unspecified) nucleoside monophosphate in which the phosphate group is esterified at the 5′ position of the glycose moiety.

NMR *or* **nmr** *abbr. for* nuclear magnetic resonance.

Nn *symbol for* the nonyl group.

Nno *symbol for* the nonanoyl group.

nNOS *see* **nitric-oxide synthase**.

No *symbol for* nobelium.

nociceptive causing pain or injury; reacting to a painful stimulus.

nociceptor any receptor that reacts to painful (i.e. nociceptive) stimuli; a pain-sense organ.

node **1** a knob, lump, or swelling; a constriction, especially when serially repeated (along the length of something). **2** *(in botany)* the point on a stem to which a leaf or a lateral branch is attached. **3** *(in physics)* a point of zero or minimum displacement in a standing wave or a system of such waves. *See also* **node of Ranvier**. —**nodal** *adj.*

node of Ranvier any of the constrictions in the myelin sheath that occur at regular intervals along the length of a myelinated nerve fibre. [After Louis Antoine Ranvier (1835–1922), French pathologist.]

NOD mice *abbr. for* nonobese diabetic mice.

nodoc *a name sometimes used for* **anticodon** (formed by reversing the letters of the word codon).

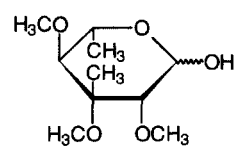
nodule bacterium *or* **nodule-forming bacterium** *a common name for* any bacterium of the genus *Rhizobium*, found as endosymbionts in root nodules. The bacterium specifically infects root cells of Leguminosae, and causes the development of **root nodules**, in which it loses its outer membrane and becomes dependent on plant metabolism. It is then morphologically differentiated from the free-living form and known as a bacteroid. In return it fixes nitrogen for the plant. *See* **nitrogenase**.

NOE *abbr. for* nuclear Overhauser effect.

NOESY *abbr. for* nuclear Overhauser effect spectroscopy.

nogalamycin an antitumour antibiotic material obtained from *Streptomyces nogalater*. It contains the carbohydrate component **nogalose**.

nogalose 6-deoxy-3-*C*-methyl-L-mannose 2,3,4-trimethyl ether; a carbohydrate component of **nogalamycin**.



noggin a dorsalizing factor localized to **Spemann's organizer** in *Xenopus laevis* embryos. Database code A43343, 222 amino acids (25.77 kDa).

noise any undesired disturbance in the signal from an instru-

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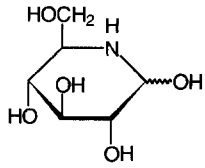
ment, or other system, that degrades the amount of useful information extractable. *Compare* **signal-to-noise ratio**.

noise analysis the technique whereby the amplitude and frequency of random fluctuations in the membrane potential of an excitable cell are used to investigate changes in conductance of single ion channels induced, e.g., by a drug or neurotransmitter.

nojirimycin 5-amino-5-deoxy-D-glucose; an antibiotic isolated from several strains of *Streptomyces*. It occurs as a pyranose-like structure with –NH– replacing the usual –O–. It inhibits intestinal α-glucosidase and pancreatic α-amylase.



nominal describing an approximate value assigned to some quantity as a guide to its real value (which may vary according to circumstances).

nomogram *or* **nomograph** any chart or diagram consisting of scaled lines and used for facilitating calculations, especially one consisting of three lines scaled for different related variables such that a straight line joining chosen values of two variables will intersect the third scale line at the related value of the third variable. —**nomography** *n.*; **nomographic** *adj.*

non+ **1** *prefix* denoting negation; absence of; opposite or reverse of; e.g. nonabsorbable, nonacylated, nonconductor, noncyclic, nonmetal, nonspecific. **2** *a variant form of* **nona+** *(sometimes before a vowel)*.

nona+ *or (sometimes before a vowel)* **non+** *comb. form* denoting nine, ninefold, nine times.

nonacosa+ *comb. form* denoting twenty-nine, twenty-nine fold, twenty-nine times.

nonacosane a linear C_{29} hydrocarbon, CH_3–$[CH_2]_{27}$–CH_3.

nonactin a neutral macrotetrolide antibiotic produced by several *Streptomyces* spp. It transports alkali cations through membranes with high selectivity for K^+, but also for NH_4^+. It is one of a related series including monactin, dinactin, and trinactin.

nonadeca+ *comb. form* denoting nineteen, nineteen fold, nineteen times.

nonaethyleneglycol mono-*n*-dodecyl ether a nonionic $C_{12}E_9$ detergent; *see* **C_xE_y**.

nonanoate *or* **pelargonoate** **1** the anion CH_3–$[CH_2]_7$–COO^-, derived from nonanoic acid (i.e. pelargonic acid). **2** any salt or ester of nonanoic acid.

nonanoyl *or* **pelargonoyl** *symbol*: Nno; the univalent acyl group CH_3–$[CH_2]_7$–CO–, derived from nonanoic acid (i.e. pelargonic acid).

nonaqueous lacking water; applied especially to solvents whether polar or nonpolar.

nonbonding electrons *an alternative name for* **lone pair**.

noncoded amino acid *or* **uncoded amino acid** any α-amino-acid residue occurring in a polypeptide or protein for which no codon exists, e.g. γ-carboxyglutamic acid, hydroxylysine, hydroxyproline, oxyproline. Residues of these amino acids are formed from residues of the corresponding coded amino acids by post-translational modification of the polypeptide chain.

noncoding region *or* **noncoding sequence** any segment of a nucleic-acid molecule for which there is no recognized gene product; it may sometimes play a structural role in the organization of the molecule. *See also* **intron**.

noncoding strand *or* **template strand** a term that is variously, and confusingly, applied to either of the two strands of genomic duplex DNA. It is now the term recommended for denoting the strand that is complementary in its sequence of bases to messenger RNA (mRNA) transcribed from the DNA; it thus functions as the template for synthesis of mRNA, which then contains the sequence present in the **coding strand** of duplex DNA (except for uracil in RNA serving in place of thymine in DNA). In some bacteria and viruses, alternate segments of both strands of duplex DNA may be noncoding. *Other names*: antisense DNA; antisense strand; complementary strand; minus strand; transcribing strand. *Compare* **complementary DNA**.

noncompetitive antagonism *(in pharmacology)* the phenomenon occurring when agonist and antagonist can be bound simultaneously, in which antagonist binding reduces or prevents the action of the agonist; e.g. channel block of the nicotinic receptor, or inhibition by adrenoceptor antagonists of the response to tyramine.

noncompetitive inhibition inhibition of an enzyme in which inhibition results from binding of the inhibitor at a different site on the enzyme surface from that at which the substrate binds, without interference with substrate binding.

nonconjugative plasmid any plasmid that cannot bring about transfer of DNA by **conjugation**.

nonconservative replication of DNA *or* **dispersive replication of DNA** *see* **replication of DNA**.

noncoupled solute translocation the translocation of a solute across a membrane that is not coupled to the translocation of another solute, in either the same or the opposite direction. *See* **facilitated diffusion, uniport**.

noncovalent describing an interaction between atoms and/or molecules that does not involve the formation of a covalent bond between them.

noncyclic electron flow *(in photosynthesis) see* **photophosphorylation**.

noncyclic photophosphorylation *see* **photophosphorylation**.

nondiffusible material material that is not diffusible in the restricted sense of its being incapable of passing through a diffusion barrier, especially through a semipermeable membrane used in dialysis. *Alternative terms recommended by IUPAC*: retentate, dialysis residue, or residue.

nondissymmetric *a term formerly used to describe* an achiral molecule that possesses an alternating axis of symmetry but that (unlike a symmetric molecule) lacks a simple axis of symmetry; the converse of **dissymmetric**. An important example is **citric acid**, which has a one-fold alternating axis but no simple axis; thus its pair of carboxymethyl groups on carbon-3 are not geometrically equivalent. *See also* **prochiral**.

nonelectrolyte any substance that is neither an electrolyte nor a conductor of electrons.

nonessential amino acid any amino acid that can be synthesized in the body in an amount corresponding to need, and hence for which there is not an absolute dietary requirement. The extent to which a particular amino acid is nonessential in any one species depends on the stage of development and physiological state of the subject. The following L-amino acids are nonessential for the maintenance of nitrogen equilibrium in an adult human: alanine, arginine, asparagine, aspartic acid, cysteine, glutamic acid, glutamine, glycine, histidine, hydroxyproline, proline, serine, and tyrosine. Arginine and histidine are, however, essential in growing children.

nonesterified fatty acid *abbr.*: NEFA; **1** *an alternative name for* **free fatty acid**. **2** *a collective term for* the total of free fatty acids in a sample, especially of blood.

nonheme iron *or (esp. Brit.)* **nonhaem iron** any iron in a biological sample or structure that is not chelated in heme groups. In nonheme-iron proteins the iron is often present in iron–sulfur clusters.

nonhistone protein *or* **nonhistone chromosome protein** any member of a highly heterogeneous group of 10–150 kDa tissue-specific proteins associated with DNA in cell nuclei. They are thought to play a part in the control of gene expression. *See also* **high mobility group proteins**.

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nonhomologous (of chromosomes or chromosome segments) not **homologous** (def. 4).

nonideal describing any gas or solution that does not behave like an ideal gas or ideal solution, respectively. —**nonideality** *n.*

Nonidet *the proprietary name for* a range of nonionic detergents that are essentially octyl- or nonyl-phenoxypolyethoxyethanols. For example, *see* **NP-40**. *Compare* **Triton**.

non-insulin-dependent diabetes *an alternative name for* type 2 **diabetes mellitus**.

noninvasive **1** not **invasive**. **2** *(of a clinical investigative technique or procedure)* carried out without penetrating the skin.

nonionic having or yielding no ions; the term is used especially of **nonionic detergents**.

nonionic detergent any detergent whose molecules cannot ionize.

non-lactose-fermenter *a jargon term for* any genus, species, or strain of microorganism that does not ferment lactose.

nonmediated transport *an alternative name for* **unmediated transport**.

non-Newtonian fluid any fluid that does not conform to **Newton's law of viscosity**, i.e. one whose (coefficient of) viscosity is not independent of flow rate.

nonose any **aldose** having a chain of nine carbon atoms in the molecule.

nonoverlapping code *see* **overlapping code**.

nonpermissive restrictive; not **permissive**.

nonpermissive cell any cell that does not support infection by a particular lytic virus; in a small percentage of instances the virus may transform a nonpermissive cell.

nonpolar **1** lacking polarity. **2** *or* **apolar** *(of a chemical group or substance)* lacking a significant permanent dipole moment.

nonpolar bond **1** any covalent bond that is not appreciably polarized. **2** *(sometimes) an alternative term for* **hydrophobic interaction**.

nonpolar solvent *a loose term denoting* any solvent with low ionizing power and hence low solvating power.

nonproductive binding *or* **dystopic binding** the binding of a substrate in an unreactive mode at the active site of an enzyme, leading to the formation of a nonproductive, or **abortive complex**.

nonproductive complex *an alternative name for* **abortive complex**.

nonprotein amino acid any amino acid that does not naturally occur as a constituent residue of proteins. Over 200 such amino acids are known to be produced in higher plants. Although they often contribute to the nitrogen pool of the plants, their specific function is unknown. Nonprotein amino acids also occur in animals but to much less degree, the most prominent examples being **argininosuccinate**, **citrulline**, and **ornithine**.

nonprotein nitrogen *abbr.*: NPN; the part of the nitrogen content of a substance (or fluid) that is not contained in the proteins present. The term is used especially of blood or serum, wherein urea accounts for about half the total NPN.

nonradioactive having no radioactivity; in practice the term is often used to refer to substances having a normal or natural nuclidic composition, ignoring any contribution from minimal proportions of naturally occurring radionuclides such as the carbon-14 content of natural organic materials.

nonradioactive tracer *(sometimes)* a labelled substance that can be detected and estimated by virtue of some property other than radioactivity (such as colour, fluorescence, or a difference in stable-isotope ratio).

nonreducing end the end of a linear oligosaccharide or polysaccharide that does not carry a potential hemiacetal or hemiketal (i.e. reducing) group.

nonsecretor *see* **secretor gene**.

nonselectively labelled describing a labelled compound in which the position(s) and the number of the labelling nuclide(s) are both undefined.

nonsense codon *or* **nonsense triplet** any one of the nucleotide triplets UAA (ochre), UAG (amber), and UGA (opal) that signal termination of translation and release of the polypeptide chain from the site of synthesis. A codon that is nonsense in one strain of an organism may nevertheless code for an amino acid in another strain containing an appropriate suppressor gene (*see* **nonsense suppressor**). UGA sometimes codes for selenocysteine and, in mitochondria, for Trp. In mitochondria AGA is a nonsense codon rather than UGA. *Compare* **missense codon**.

nonsense mutation any mutation in a DNA molecule that results in an alteration of a sense codon to a **nonsense codon** in the mRNA transcript, the translation of which leads to the formation of a truncated polypeptide gene product. *Compare* **missense mutation**.

nonsense suppressor any tRNA molecule that is able to insert an amino-acid residue into a growing polypeptide chain at a nonsense codon in an mRNA molecule. It has an altered anticodon, produced as a result of a **suppressor mutation**.

nonshivering thermogenesis *abbr.*: NST; a mechanism of rapid heat production in response to cold that does not involve muscular contractions. It is important during the neonatal period, during cold adaptation of a number of small mammals, and during the arousal period of animals that hibernate. Heat is produced in the mitochondria of brown adipose tissue in response to the presence in the inner mitochondrial membrane of a specific 32 kDa protein. This protein uncouples the respiratory chain and is inducible by norepinephrine. It is known as **brown fat uncoupling protein**.

nonsuppressible insulin-like activity *abbr.*: NSILA; **insulin-like activity** that is not suppressible by specific antisera to insulin. The activity in serum was once thought to be in two protein fractions: a minor component (*abbr.*: $NSILA_s$), soluble in acidic aqueous ethanol; and a major component (*abbr.*: $NSILA_p$), precipitable by acidic aqueous ethanol and now known to be an artefact. The activity is now attributed to **insulin-like growth factors**.

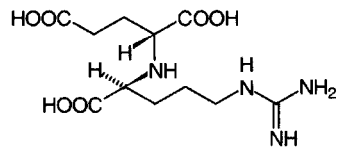
nontranscribing strand (of duplex DNA) *see* **coding strand**.

nonulose any **ketose** having a chain of nine carbon atoms in the molecule.

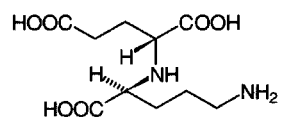
nonyl *symbol*: Nn; the alkyl group $CH_3[CH_2]_7CH_2–$, derived from nonane.

nonyl glucoside *n*-nonyl-*β*-D-glucopyranoside; a mild, nonionic detergent, CMC 6.5 mM. *Compare* **heptyl glucoside**, **hexyl glucoside**, **octyl glucoside**.

nopaline *N*-(1-carboxy-4-guanidinobutyl)glutamic acid; N^2-(1,3-dicarboxypropyl)arginine; a rare amino-acid derivative that is produced by a certain type of crown-gall tissue (*see* **crown-gall disease**); one of a group of **opines**. The genes responsible for the synthesis of nopaline are part of the **T-DNA** from a **Ti-plasmid**.



nopalinic acid *or* **ornaline** *N*-(1-carboxy-4-aminobutyl)glutamic acid; N^2-(1,3-dicarboxypropyl)ornithine; one of a group of **opines** found in plant tumours occurring in **crown-gall disease**.



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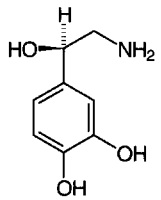
nor+ *prefix (in chemical nomenclature)* denoting **1** replacement of one side-chain methyl group by a hydrogen atom, e.g. norepinephrine, 19-nortestosterone. Replacement of two or three methyl groups is denoted by the prefix dinor+ or trinor+, respectively (in terpene nomenclature the prefix nor+ formerly denoted removal of all replaceable methyl groups; hence, e.g., 8,9,10-trinorbornane was formerly known as norbornane). **2** elimination of one methylene group from a chain or ring of carbon atoms; it is used especially for steroids, e.g. 23-nor-5β-cholanoic acid, A-nor-5β-androstane, norophthalmic acid. Elimination of two or three methylene groups is denoted by the prefix dinor+ or trinor+, respectively. **3** an isomer with an unbranched hydrocarbon chain, e.g. norleucine, norvaline; use discouraged.

noradrenaline *an alternative name for* **norepinephrine**.

noradrenergic *(sometimes)* **1** an (adrenergic) nerve cell that itself liberates noradrenaline (i.e. **norepinephrine**). **2** a cell or receptor that is stimulated preferentially by norepinephrine. —**noradrenergically** *adv.*

norepinephrine *or* **noradrenaline** *or* **levarterenol** (–)-(3,4-dihydroxyphenyl)-2-aminoethanol; a hormone secreted by the adrenal medulla, and a neurotransmitter in the sympathetic peripheral nervous system and in some tracts in the central nervous system. It is also the demethylated biosynthetic precursor of epinephrine in the adrenal medulla. It has a powerful lipolytic action, mediated by cyclic AMP, and is an agonist for **adrenoceptors**, inducing arteriolar constriction and raised systolic and diastolic arterial blood pressure.



R-(–)-enantiomer

Norit *the proprietary name for* a commercially produced activated carbon, useful as an adsorbent.

norleucine *symbol*: Ahx *or (formerly)* Nle; 2-aminohexanoic acid; a nonprotein α-amino acid. *See also* **nor+** (def. 3).

norm+ *a variant form of* **normo+** *(before a vowel)*.

normal **1** not deviating from an established pattern; approximating to an average, or within the usual range (of values). **2** *(in organic chemistry) symbol*: N; (of a solution) containing one **equivalent** (def. 4) of a specified substance (of specified equivalence factor) in one litre of solution. Use now not recommended. **3** *(in organic chemistry)* a chemical compound that has an unbranched chain of carbon atoms; the names of such compounds may be prefixed by '*n*', as in *n*-butane. However, this is not the currently recommended terminology. **4** *(in biology)* not diseased or not having been exposed to an experimental procedure. **5** *(in mathematics)* (of a straight line or plane) at a right angle (to another straight line or plane).

normal distribution *or* **Gaussian distribution** any continuous frequency distribution of events, observations, etc. characterized by a symmetrical bell-shaped curve of the frequency of x, $f(x)$, against the value of x, that is represented by the equation:

$$f(x) = [1/\sigma(2\pi)^{0.5}]e^{-(x-\mu)^2/2\sigma^2}$$

where μ is the mean and σ is the standard deviation.

normality *(in chemistry)* the chemical concentration of a solution expressed as the number of **equivalents** (def. 4) of a specified substance (of specified equivalence factor) per litre. Use now not recommended.

normal range *(in clinical chemistry)* the range of values of a particular characteristic within which 95 percent of observations made on presumed normal healthy individuals fall. It is useful as a reference in the investigation of disease.

normal saline *an alternative and less suitable name for* **physiological saline**.

normal solution a solution in which the amount-of-substance concentration of the **equivalent** (def. 3) of the reagent is one mole per litre; the equivalence factor of the reagent should be specified. Not now recommended. *See also* **normal** (def. 2).

normal temperature and pressure *abbr.*: NTP *or* N.T.P. *or* ntp; *a former term for* **standard temperature and pressure**.

normetadrenaline *an alternative name for* **normetanephrine**.

normetanephrine *or* **normetadrenaline** 3-*O*-methylnorepinephrine; an inactive metabolite of norepinephrine produced by the action of **catechol *O*-methyltransferase**.

normo+ *or (before a vowel)* **norm+** *comb. form* denoting normal; used especially in biology and medicine to indicate within the normal range. *See also* **eu+**.

normoblast a normal precursor cell to an erythrocyte, characterized by condensation of the nucleus into a homogeneous densely staining body. Normoblasts are normally found only in hemopoietic tissue. —**normoblastic** *adj.*

normocyte an erythrocyte of normal colour, shape, and size. —**normocytic** *adj.*

normoglycemia *or (esp. Brit.)* **normoglycaemia** *an alternative term for* **euglycemia**. —**normoglycemic** *or (esp. Brit.)* **normoglycaemic** *adj.*

normotensive having an arterial blood pressure within the normal range for the particular group to which the subject belongs.

Norrish, Ronald George Wreyford (1897–1978), British physical chemist; Nobel Laureate in Chemistry (1967) jointly with G. Porter, the prize being shared with M. Eigen 'for their studies of extremely fast chemical reactions, effected by disturbing the equilibrium by means of very short pulses of energy'.

norsteroid any steroid that, relative to a parent compound, lacks either one axial methyl group or one methylene group in a side chain, or that has one ring contracted by one carbon atom. *See also* **nor+**.

Northern blotting *or* **Northern transfer** any **blotting** in which the primary electrophoresis is performed with RNA, which is subsequently hybridized to radioactive DNA. The term was coined to distinguish the process from **Southern blotting**, which is performed with DNA.

Northrop, John Howard (1891–1987), US biochemist and protein chemist; Nobel Laureate in Chemistry (1946) jointly with W. M. Stanley 'for their preparation of enzymes and virus proteins in a pure form' [prize shared with J. B. Sumner].

norvaline *symbol*: Avl (from aminovaleric) *or* Ape (from aminopentanoic) *or (formerly)* Nva; 2-aminovaleric acid (now the preferred trivial name); 2-aminopentanoic acid; a nonprotein α-amino acid. *See also* **nor+** (def. 3).

NOS *abbr. for* **nitric-oxide synthase**.

noso+ *or (before a vowel)* **nos+** *comb. form* indicating disease.

nosocomial **1** associated with a hospital. **2** a disorder (e.g. an infection) acquired during a hospital stay that is unrelated to the primary condition of the patient. A nosocomial infection can refer to hospital workers as well.

nosogenesis *an alternative term for* **pathogenesis**. —**nosogenic** *or* **nosogenetic** *adj.*

nosography a written systematic classification and description of diseases.

nosology the branch of medicine dealing with the classification of diseases.

notatin *a name sometimes still used for* glucose oxidase. Notatin was so called because it is produced in considerable quantity by some microfungi, e.g. *Penicillium notatum*.

notch a gene, found in *Drosophila*, that encodes a protein essential for the proper differentiation of ectoderm. Expression of the *notch* gene is under the control of neurogenic genes. The

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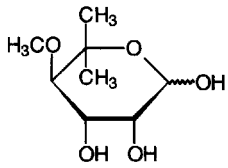
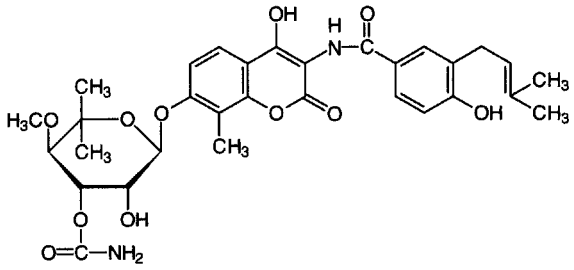
gene product is a transmembrane protein with 36 EGF-like repeats; database code NOTC_DROME, 2703 amino acids (288.81 kDa).

notexin a **phospholipase** A_2 (EC 3.1.1.4) from snake venom that acts as a presynaptic neurotoxin. The reaction is Ca^{2+}-dependent. Example (precursor) from the Australian tiger snake, *Notechis scutatus scutatus*: database code PA2 3_NOTSC, 119 amino acids (13.66 kDa); 3-D structure known.

noviose 6-deoxy-5-*C*-methyl-L-*lyxo*-hexose 4-methyl ether; a carbohydrate component of **novobiocin**.



novobiocin an antibiotic produced by *Streptomyces spheroides*, *S. niveus*, and certain other species; it is active against Gram-positive and some Gram-negative bacteria. In susceptible organisms it is a specific inhibitor of **(DNA) gyrase**, interacting with the B subunit, and thereby interfering with DNA synthesis.



noxa (*pl.* **noxae**) anything that is harmful to living organisms. —**noxious** *adj.*

Np *symbol for* neptunium.

NP-40 polyethyleneglycol-*p*-isooctylphenyl ether; a polyoxyethylene nonionic detergent, CMC 0.05–0.3 mM. *Proprietary name*: Nonidet P40.

NPC *abbr. for* neural precursor cell (*see* **Nedd**).

NPN *abbr. for* nonprotein nitrogen.

NPY *abbr. for* neuropeptide Y.

nRNA *abbr. for* nuclear RNA.

NR protein *abbr. for* nitrogen regulatory protein.

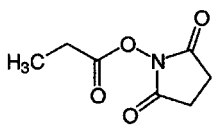
ns *symbol for* nanosecond (i.e. 10^{-9} s).

NSF *abbr. for* National Science Foundation (of the USA).

NSF protein *abbr. for N*-ethylmaleimide-sensitive fusion protein.

NSILA *abbr. for* nonsuppressible insulin-like activity.

NSP *abbr. for N*-succinimidyl propionate, a propionylating agent.



NST *abbr. for* nonshivering thermogenesis.

NT *abbr. for* neurotrophin.

N terminus *or sometimes* **N terminal** the end of any peptide chain in any (poly)peptide or protein at which the 2-amino function of a constituent α-amino acid (or the 2-imino function of an α-imino carboxylic acid) is not attached in peptide linkage to another amino-acid residue. This function may bear an acyl group or other function in nonpeptide linkage; when it is a free amino group (and also protonated and positively charged at neutral or acidic pH values), the chain end may then be alternatively termed the **amino terminus** (*or* NH_2 terminus) or **amino terminal** (*or* NH_2 terminal). However, 'amino terminus' is often used loosely for any N terminus. *Compare* **C terminus**. —**N-terminal** *adj.*

NTP **1** *abbr. for* any (unknown or unspecified) nucleoside (5′-)triphosphate. **2** *(in clinical biochemistry) abbr. for* 5′-nucleotidase (EC 3.1.3.5). **3** *or* N.T.P. *or* ntp; *abbr. for* normal temperature and pressure; stp (i.e. standard temperature and pressure) now used.

NTPase *abbr. for* nucleoside triphosphatase.

NTP polymerase *see* **polynucleotide adenylyltransferase**.

nu *symbol*: ν (lower case) *or* N (upper case); the thirteenth letter of the Greek alphabet. For uses *see* **Appendix A**.

nu body *or* **ν body** *or* **deoxyribosome** a type of spheroid particle seen on electron-microscopic examination of chromatin; now thought to be the same as a **nucleosome**.

Nuc *symbol for* an undetermined, unidentified, or unspecified nucleoside residue; alternative to N.

nucle+ *a variant for of* **nucleo+** *(before a vowel)*.

nuclear **1** of, pertaining to, or contained within the nucleus of a cell. **2** of, pertaining to, or concerning an atomic nucleus. **3** of, pertaining to, or operated by energy derived from fission or fusion of atomic nuclei.

nuclear area *an alternative name for* **nucleoid** (def. 2).

nuclear atom *or* **central atom** (of a coordination entity) the atom to which all other atoms are directly attached.

nuclear body *an alternative name for* **nucleoid** (def. 2).

nuclear division *or* **nuclear fission** the division of the nucleus of a cell, especially by **mitosis** or **meiosis**.

nuclear emulsion a fine-grained photographic emulsion designed for recording the tracks of subatomic particles within it.

nuclear envelope *or* **nuclear membrane** the membrane that surrounds the nucleus of a eukaryotic cell. It is a double membrane composed of two lipid bilayers separated by a gap of width 20–40 nm (the perinuclear space). The outer nuclear membrane is continuous with the endoplasmic reticulum of the cell and is sometimes studded with ribosomes. At specialized regions (**nuclear pores**) the outer nuclear membrane is connected to the inner nuclear membrane.

nuclear filament-related protein *abbr.*: NUF1; an essential component of the nucleoskeleton with a role in crosslinking filaments or anchoring other molecules. Example from yeast: database code NUF1_YEAST, 944 amino acids (111.66 kDa).

nuclear fission **1** *(in biology) an alternative term for* **nuclear division**. **2** *(in physics) see* **fission** (def. 1).

nuclear fraction *an operational term for* the material deposited by low-speed centrifugation of a homogenate of eukaryotic cells or tissue. It consists predominantly of nuclei together with unbroken cells.

nuclear fusion **1** *(in biology)* the **fusion** (def. 3) of the nuclei of a heterokaryon leading to the formation of a hybrid cell. **2** *(in physics) see* **fusion** (def. 4).

nuclear isomer *(in physics) see* **isomer** (def. 2).

nuclear lamina the electron-dense layer lying on the nucleoplasmic side of the inner membrane of a cell nucleus. The polypeptides of the lamina are thought to be concerned in the dissolution of the nuclear envelope and its re-formation during mitosis.

nuclear localization signal *abbr.*: NLS; a sequence of amino acids seven to nine residues long within a protein, normally at sites away from the N or C terminus, that acts as a signal for the localization of the protein within the nucleus. Characteristically, NLSs are rich in basic residues, but include also one or more prolines.

nuclear magnetic resonance *abbr.*: NMR *or* nmr; the phenomenon that occurs when atomic nuclei that possess a mag-

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netic moment are placed in a constant magnetic field of high intensity and are simultaneously exposed to electromagnetic radiation of an appropriate frequency in the radiofrequency region, whereby the nuclei are caused to change from a low-energy to a high-energy state with the absorption of energy. Nuclei that display this phenomenon include those of the nuclides protium, tritium, carbon-13, nitrogen-15, fluorine-19, and phosphorus-31; all these nuclei have nonzero spins and, therefore, magnetic moments. *See also* **nuclear magnetic resonance spectroscopy**.

nuclear magnetic resonance spectroscopy *abbr.*: NMR spectroscopy *or* nmr spectroscopy; absorption spectroscopy in the radiofrequency region based on the phenomenon of **nuclear magnetic resonance**. Unless otherwise qualified the term usually denotes nuclear magnetic resonance spectroscopy of protium atoms, also known as proton magnetic resonance spectroscopy (*abbr.*: pmr spectroscopy). Nuclei of the same nuclide in different chemical environments give rise to distinguishable spectral lines, the positions, intensities, widths, and multiplicities of which give considerable information about the structure of complicated molecules containing such nuclei. The technique is also useful for determination of the concentrations of particular substances in complex environments, including that of an intact mammal. *Compare* **electron spin resonance spectroscopy**, **magnetic resonance imaging**.

nuclear magneton *symbol*: μ_N; a quantity of magnetic moment, given by $\mu_N = eh/4\pi m_p = (m_e/m_p)\mu_B$, where e is the elementary charge, h is the Planck constant, m_e and m_p are the rest masses of an electron and a proton respectively, and μ_B is the **Bohr magneton**. It is a fundamental physical constant, of value $5.050\ 786\ 6(17) \times 10^{-27}$ J T^{-1}.

nuclear matrin *see* **matrin**.

nuclear medicine the branch of medicine concerned with the use of radioactive nuclides for diagnosis or treatment of disease, or for medical research.

nuclear membrane *an alternative name for* **nuclear envelope**.

nuclear mitotic apparatus protein *abbr.*: NuMA; one of a family of abundant coiled-coil nuclear proteins located in the nucleus during interphase, but which, when the nuclear envelope disassembles in prometaphase, rapidly redistribute to the developing spindle poles. Example from human: database code S33414, 45 amino acids (4.73 kDa) (one of multiple forms).

nuclear Overhauser effect *or* **nuclear Overhauser enhancement** *abbr.*: NOE; in nuclear magnetic resonance spectroscopy, a phenomenon in which saturation of an electron resonance by the simultaneous application of a radiofrequency field causes, under appropriate conditions, a considerable increase in the polarization of the interacting nuclei and hence in the NMR signal produced.

nuclear Overhauser effect spectroscopy *abbr.*: NOESY; in **nuclear magnetic resonance spectroscopy** advantage can be taken of the fact that the energy states of the spins of two nuclei subject to the **nuclear Overhauser effect** (NOE) are slightly perturbed by the mutual dipolar coupling (the effects of J-coupling are ignored). A perturbation of the populations of the states of one of the spins will lead to a transfer of the populations between the upper and lower energy states of the second spin, thereby modifying the resonance intensity. The NOE can be either positive or negative depending on the nuclei involved and the rapidity of the relative motions of the two spins. The strength of the dipolar coupling is distance dependent. Thus measurements of the NOE between two nuclei can lead to the estimation of the distance between them. Conversely, if the distance between the two nuclei is fixed (e.g. in a bond), then the NOE measurement can yield an indication of the dynamic motions in the molecule. Two-dimensional spectroscopy, known as 2D NOESY, is used to elucidate dipolar coupling networks present in complex biomolecules, using the NOEs between individual ^{1}H nuclei in the molecule. The network of NOEs obtained provides a basis for the determination of the three-dimensional structure in solution. Applications include the structures of small proteins and nucleic acids as well as protein–drug and protein–nucleic acid complexes.

nuclear pore any of the numerous similar discrete openings in the **nuclear envelope** of a eukaryotic cell, where the inner and outer nuclear membranes are joined. The nuclear pores are the central feature of a complex which has a mass of ≈125 MDa in higher eukaryotes and are estimated to contain about 100 different polypeptides. The complex constitutes a diffusion channel about 9 nm in diameter through which proteins enter the nucleus and ribonucleoproteins leave. Small proteins enter freely but the entry of larger proteins is controlled by a mechanism of active transport. Such proteins contain within their primary structure one or more clusters of basic amino acids which comprise the nuclear localization sequence (*abbr.*: NLS). Two steps are involved: binding to the nuclear envelope, followed by energy-dependent transit through the complex. Four soluble proteins have been shown to assist in the process: karyopherin α, *other name*: importin α (the NLS receptor), karyopherin β, *other name*: importin β (which mediates binding to the nuclear pore complex), a small guanosine triphosphatase (*abbr.*: GTPase), Ran, and p10/NTF2 (a protein of hitherto ill-defined function but now claimed to coordinate the Ran-dependent association and disassociation reaction). Ran cycles between a GDP- and GTP-bound form and is thereby involved in the consumption of energy for the protein import. The exchange factor for Ran (RCC1) is located inside the nucleus whereas its GTPase-activating protein (Rab-GAP1 or RAN1) is cytoplasmic. Much less is known about the mechanism whereby the export of ribonucleoprotein is controlled. RNA itself does not seem to leave the nucleus.

nuclear rest *see* **nucleoid** (def. 4).

nuclear transformation transformation of a nuclide; the change of one nuclide into another.

nuclease any enzyme within subclass EC3.1, that catalyses the hydrolysis of ester linkages in nucleic acids. Nucleases with sugar specificity are referred to as ribonucleases or deoxyribonucleases; **endonucleases** create internal breaks, while 5′- and 3′-**exonucleases** remove nucleotide residues from the indicated end. Some nucleases are specific for double- or single-stranded nucleic acids.

nucleate **1** *or* **nucleated** possessing a nucleus. **2** to form, to act as, or to provide with, a nucleus or nuclei. **3** any salt of a nucleic acid.

nucleation **1** the act or process of nucleating or forming a nucleus. **2** *(in chemistry)* **a** the aggregation of molecules to form a polymer or a new phase within a medium. **b** (*also known as* **seeding**) the addition of a small quantity of finely divided crystalline material to a supersaturated solution in order to promote crystallization.

nuclei the plural of **nucleus**.

nucleic acid *abbr.*: NA; any single- or double-stranded polynucleotide of molar mass in the range 20 kDa to 40 GDa or more. Nucleic acids are either **deoxyribonucleic acids** (DNA) or **ribonucleic acids** (RNA). The phosphoric residue linking any constituent mononucleotide residue to the next bears one free hydroxyl group, which is weakly acidic. They are universal constituents of living matter and are concerned with the storage, transmission, and transfer of genetic information.

nucleics *an informal collective term sometimes used for* nucleotides, nucleosides, and nucleobases, whether constituents of nucleic acids or compounds of low M_r, and including their metabolic relatives and synthetic analogues.

nuclein the name given by J. F. Miescher (1844–95) to an unusual phosphorus-containing material that he was able to isolate from the nuclei of pus cells, now known to have been **nucleoprotein**.

nucleinase *a name once proposed to designate* the enzymes now known as **nucleases**.

nucleo+ *or (before a vowel)* **nucle+** *comb. form* denoting **1** nucleus or nuclear. **2** nucleic acid.

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nucleobase any nitrogenous base that is a constituent of a nucleoside, nucleotide, or nucleic acid.

nucleobindin a DNA-binding protein containing a signal peptide, leucine zipper, and basic amino acid-rich regions. It was derived from a cell line from the lupus erythematosus-prone mouse MRL/T. Example (precursor) from human: database code NUBN_HUMAN, 460 amino acids (53.67 kDa).

nucleocapsid the structure within a virus that comprises the proteinaceous capsid and the genomic nucleic acid. In enveloped viruses the nucleocapsid is surrounded by an envelope.

nucleocidin 4′-*C*-fluoroadenosine 5′-sulfamate; an analogue of adenylate produced by *Streptomyces calvus*, and the first naturally occurring derivative of a fluorosugar to be described. It has antibiotic activity against trypanosomes and inhibits translation in both eukaryotic and prokaryotic systems.

nucleocytoplasmic (of a structure or process) occurring between the nucleus and the cytoplasm; (of a property) relating the nucleus to the cytoplasm.

nucleodisome a structure consisting of two **nucleosomes** and isolable under certain conditions from some forms of chromatin.

nucleohistone any nucleoprotein consisting of DNA and histone(s).

nucleoid **1** resembling a nucleus. **2** the part or parts of a prokaryotic cell containing the genome and functionally equivalent to the nucleus of a eukaryotic cell. The meaning is sometimes extended to include the electron-dense inner zone observable in certain viruses. *Other names*: bacterial nucleus; chromatinic body; karyoid; nuclear area; nuclear body; nucleoid body; prokaryon. **3** the nucleus-like structure liberated from a eukaryotic cell by mild lysis. It contains histone-free supercoiled DNA within a flexible cage of RNA and protein. **4** *or* **nuclear rest** the nuclear residue sometimes observable in an erythrocyte. **5** the very dense core of a **microbody**.

nucleolar DNA *or* **ribosomal DNA** the DNA comprising the **nucleolar organizer(s)**.

nucleolar organizer *or* **nucleolus organizer** the portion of the genome of a eukaryotic cell that is associated with the **nucleolus** and contains the genes from which 45S ribosomal-precursor RNA is transcribed.

nucleolar phosphoprotein B23 *or* **nucleophosmin** *or* **numatrin** a monomeric, or under some conditions disulfide-linked dimeric, nucleolar protein that binds to single-stranded nucleic acids and may be bound to rRNA in the nucleolus. Example (precursor) from human: database code B232_HUMAN, 294 amino acids (32.54 kDa).

nucleolin *or* **protein C23** the major nucleolar protein of growing eukaryotic cells believed to function in pre-rRNA processing and ribosome assembly. It is a phosphoprotein found associated with intranucleolar chromatin and periribosomal particles. Example from human: database code NUCL_HUMAN, 706 amino acids (76.13 kDa).

nucleolus (*pl.* **nucleoli**) a small, dense body one or more of which are present in the nucleus of eukaryotic cells. It is rich in RNA and protein, is not bounded by a limiting membrane, and is not seen during mitosis. Its prime function is the transcription of the nucleolar DNA into 45S ribosomal-precursor RNA, the processing of this RNA into 5.8S, 18S, and 28S components of ribosomal RNA, and the association of these components with 5S RNA and proteins synthesized outside the nucleolus. This association results in the formation of ribonucleoprotein precursors; these pass into the cytoplasm and mature into the 40S and 60S subunits of the ribosome. —**nucleolar** *adj.*

nucleolytic capable of causing hydrolysis of nucleic acid.

nucleon a neutron or a proton.

nucleonics the branch of physics concerned with the practical applications of nuclear phenomena.

nucleon number *or* **mass number** *symbol*: *A*; a dimensionless physical quantity, having an integral value for any given nuclide, equal to the total number of nucleons (i.e. protons and neutrons) contained in the nucleus of an atom of the nuclide; it also is the integer nearest to the numerical value of the relative atomic mass of that nuclide and is equal to the arithmetical sum of the **neutron number**, *N*, of the nuclide and the **proton number**, *Z*, of the relevant chemical element: i.e. $A = N + Z$. The nucleon number may be attached to the symbol for the chemical element as a left superscript, or to the name of the element as a suffix; e.g. ^{14}C, or carbon-14.

nucleophile or **nucleophilic reagent** any reagent that is preferentially attracted to a region of low electron density in a chemical reaction. *Compare* **electrophile**.

nucleophilic **1** of, pertaining to, or being a **nucleophile**; having or involving an affinity for regions of low electron density in a chemical reactant. **2** describing a chemical reaction in which a nucleophilic reagent participates.

nucleophilic catalysis catalysis by a **Lewis base**, which donates an electron pair to the reactant.

nucleophilic displacement *an alternative term for* **nucleophilic substitution reaction**.

nucleophilicity the relative reactivity of a nucleophile, measured in terms of the relative rate constants of different nucleophiles towards a common reactant.

nucleophilic reagent *an alternative term for* **nucleophile**.

nucleophilic substitution reaction *or* **nucleophilic displacement** a chemical reaction in which a **nucleophile** effects heterolytic substitution in another reactant, both bonding electrons being supplied by the nucleophile.

nucleophosmin *see* **nucleolar phosphoprotein B23**.

nucleoplasm all the protoplasm contained within the nuclear envelope of a living cell. —**nucleoplasmic** *adj.*

nucleoplasmin a heat-stable acidic protein present in the nucleoplasm of many cell types. It forms complexes with histones and functions in the assembly of nucleosomes in the formation of chromatin. Example from *Xenopus laevis*: database code NUPL_XENLA, 200 amino acids (22.02 kDa).

nucleoprotamine any nucleoprotein consisting of DNA and protamine(s).

nucleoprotein any complex of a protein with a deoxyribonucleic acid (**deoxyribonucleoprotein**) or a ribonucleic acid (**ribonucleoprotein**).

nucleosidase any enzyme that hydrolyses the *N*-glycosidic bond in a **nucleoside** (or in a nucleotide or some other derivative of a nucleoside). Such enzymes are classified within the sub-subclass EC 3.2.2, i.e. enzymes that hydrolyse *N*-glycosyl compounds.

nucleoside **1** *symbol* (for a residue of an undetermined, unknown, or unspecified nucleoside): N *or* Nuc; any **glycosylamine** that is a component of a nucleic acid and that consists of a nitrogenous base linked either to β-D-ribofuranose (forming a ribonucleoside, as in RNA) or to 2-deoxy-β-D-ribofuranose (forming a deoxyribonucleoside, as in DNA). The base is either a purine (linked at N-9) or a pyrimidine (linked at N-1, or in the case of pseudouridine at C-5). **2** any compound that is a glycosylated heterocyclic nitrogenous base; the glycose moiety commonly is ribose, but is sometimes a different sugar or a modified sugar; e.g. cytarabine (1-β-D-arabinofuranosylcytosine).

nucleoside antibiotic any of a group of **nucleosides** (def. 2) that are not components of nucleic acids but are produced by various microorganisms and fungi (especially *Streptomyces* spp.), and have antibiotic activity. They contain unusual nitrogenous bases and/or unusual sugars (or sugar derivatives), and may also contain one or more additional components. Examples include **cordycepin**, **nucleocidin**, **puromycin**, and **showdomycin**.

nucleoside cyclic phosphate *or* **cyclic nucleotide** any nucleotide that consists of a nucleoside doubly esterified with one [ortho]phosphate molecule on its glycose moiety (usually at the 3′ and 5′positions, but sometimes at the 2′- and 3′-positions) e.g. cyclic AMP.

nucleoside diphosphatase EC 3.6.1.6; *systematic name*: nuc-

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leoside diphosphatase phosphohydrolase; an unspecific enzyme that hydrolyses a number of nucleoside diphosphates to a nucleoside monophosphate and orthophosphate. Substrates include IDP, GDP, UDP, and D-ribose 5-phosphate. There is also the more specific **guanosine-diphosphatase**, EC 3.6.1.42; *systematic name*: GDP phosphohydrolase, which hydrolyses guanosine diphosphate to guanylic acid and orthophosphate; example from yeast: database code GDA1_YEAST, 518 amino acids (56.76 kDa).

nucleoside diphosphate any nucleotide that consists of a nucleoside esterified with diphosphate on its glycose moiety (usually at the 5′ position, when the symbol is NDP).

nucleoside diphosphate reductase EC 1.17.4.1; *recommended name*: ribonucleoside-diphosphate reductase; *systematic name*: 2′-deoxyribonucleoside-diphosphate:oxidized thioredoxin 2′-oxidoreductase; *other name*: ribonucleotide reductase. A nucleotide reductase enzyme, present in most organisms, that catalyses the formation of a 2′-deoxyribonucleoside diphosphate, oxidized thioredoxin, and H_2O from a ribonucleoside diphosphate and reduced thioredoxin. It requires iron and ATP. The enzyme from *Escherichia coli* is formed from B2 protein (dimer of β chains; Fe-binding subunit, 3-D structure known) and B1 (dimer of α chains), which contains a disulfide/sulfhydryl redox system; it is the enzyme responsible for the biosynthesis of deoxyribonucleotides from ribonucleotides, e.g. in *de novo* biosynthesis. The B2 dimer contains two Fe(III) ions (one on each monomer) that form a Fe^{3+}–O–Fe^{3+} group. This forms a free radical centre (involving an enzyme tyrosyl residue) that abstracts a hydrogen from the ribose (ultimately from the 2′ position, but the mechanism is complex). This leads to loss of the 2′–OH. Hydride ions are lost from enzyme sulfhydryl groups to react with these OH· groups to form water, resulting in formation of disulfide groups. The hydrogen abstracted by the free radical centre is returned to what now becomes 2′-deoxyribose. The enzyme's disulfide groups are reduced in turn by thioredoxin. There is an allosteric site on the B1 subunit dimer; ATP acts at this site as an activator and dATP as an inhibitor, in a complex interaction with a second site that determines the specificity of the enzyme towards different nucleotides. Example from *E. coli*, α chain: database code RIR1_ECOLI, 761 amino acids (85.64 kDa); β chain: database code RIR2_ECOLI, 375 amino acids (43.34 kDa). A **nucleoside triphosphate reductase** is produced when the organisms are growing anaerobically.

nucleosidediphosphosugar *or* **nucleoside diphosphate sugar** *or* **nucleotide sugar** any **nucleotide** (def. 2) in which the distal phosphoric residue of a nucleoside 5′-diphosphate is in glycosidic linkage with a monosaccharide (or a derivative of a monosaccharide).

nucleoside monophosphate *see* **nucleoside phosphate**.

nucleoside phosphate *or* **nucleoside monophosphate** any nucleotide that consists of a nucleoside esterified with [ortho]phosphate on its glycose moiety (usually at the 5′-position, when the symbol is NMP).

nucleoside-triphosphatase *abbr.*: NTPase; EC 3.6.1.15; an unspecific diphosphate phosphohydrolase enzyme that catalyses the hydrolysis of the distal diphosphate bond in various nucleoside triphosphates, with formation of [ortho]phosphate and the corresponding nucleoside diphosphate. It acts also on certain other diphospho-compounds.

nucleoside triphosphate any nucleotide that consists of a nucleoside esterified with triphosphate on its glycose moiety (usually at the 5′-position, when the symbol is NTP).

nucleoside triphosphate reductase EC 1.17.4.2; *recommended name*: ribonucleoside-triphosphate reductase; *systematic name*: 2′-deoxyribonucleoside-triphosphate:oxidized thioredoxin 2′-oxidoreductase. A nucleotide reductase enzyme found in *Lactobacillus leichmannii* (and presumably related organisms). It catalyses the formation of a 2′-deoxyribonucleoside triphosphate, oxidized thioredoxin, and H_2O from a ribonucleoside triphosphate and reduced thioredoxin. It requires cobalt and ATP. Example from *L. leichmannii*: database code LBARTR, 739 amino acids (81.85 kDa).

nucleosome a particle that forms the primary packing unit of DNA in chromatin. Nucleosomes give electron micrographs of decondensed chromatin a 'beads-on-a-string' appearance, and are released on mild digestion of eukaryotic nuclei with micrococcal endonuclease. Each consists of a segment of duplex DNA, 160–240 base pairs long, with associated **histone**; about 146 base pairs of the DNA comprise a **core particle** and the remainder form the linker DNA. The core particle is a disklike structure, 11 nm in diameter and 5.7 nm thick, consisting of two molecules each of histones H2A, H2B, H3, and H4 with approximately two superhelical turns of double-stranded DNA wound round it. In the intact nucleosome, an average of one molecule of histone H1 is on the exterior of each core particle and appears to mediate the packing together of adjacent nucleosomes in condensed chromatin. *See also* **nu body**.

nucleotidase any phosphoric monoester hydrolase enzyme that catalyses the hydrolysis of a **nucleotide** (def. 1, 2) to yield a nucleoside and orthophosphate. The principal ones are classified under three EC numbers (1) EC 3.1.3.31; *recommended name*: nucleotidase; enzymes having a wide specificity for 2′-, 3′-, and 5′-nucleotides, and that also hydrolyse glycerol phosphate and 4-nitrophenyl phosphate; (2) EC 3.1.3.6; *recommended name*: 3′-nucleotidase; an enzyme having a wide specificity for 3′-ribonucleotides; these enzymes hydrolyse a 3′-ribonucleotide to a ribonucleoside and orthophosphate. Some such enzymes are not sugar specific. Example, nuclease PA3 (deoxyribonuclease PA3) from *Penicillium* sp: database code NUP3_PENSQ, 270 amino acids (29.18 kDa). (3) EC 3.1.3.5; *recommended name*: 5′-nucleotidase; an enzyme having a wide specificity for 5′-ribonucleotides. These enzymes hydrolyse a 5′-ribonucleotide to a ribonucleoside and orthophosphate. Example, (precursor) human ecto-nucleotidase (CD73): database code 5NTD_HUMAN, 574 amino acids (63.29 kDa).

nucleotide **1** *or* **mononucleotide** *or* **nucleoside [mono]phosphate** any compound that consists of a **nucleoside** (def. 1) esterified with [ortho]phosphate at either the 3′- or the 5′-hydroxyl group of its glycose moiety (ribonucleosides giving **ribonucleotides**, and deoxyribonucleosides giving **deoxyribonucleotides**). Nucleotides are the constitutional units into which nucleic acids are broken down by partial hydrolysis and from which they are considered to be built up. **2** any compound consisting of a **nucleoside** (def. 2) that is esterified with [ortho]phosphate or an oligophosphate at any hydroxyl group on its glycose moiety. In this sense the term includes **nucleoside cyclic phosphate**, **nucleoside diphosphate**, **nucleoside diphosphosugar**, **nucleoside triphosphate**, and pyridine nucleotide. **3** any compound containing a moiety of a nucleotide (def. 1, 2). Included are: any carrying an additional phosphoric group at another position on the glycose moiety; any formed (actually or conceptually) from two or more such nucleotides, whether the same or not, joined together in phosphoric-ester linkage (to form an **oligonucleotide** or a **polynucleotide**); and, in certain instances, any formed from such a nucleotide joined through a phosphoric anhydride link either to a second nucleotide or to some other phosphate ester. Exceptionally, the term includes also certain analogous compounds (especially flavin mononucleotide, and hence also flavin-adenine dinucleotide) that, being derivatives of ribitol, are not true nucleoside phosphates or else are not formed exclusively from them.

nucleotide-binding fold *or* **nucleotide-binding pocket** a common structural feature that is possessed by numerous dehydrogenase enzymes utilizing either of the nucleotide coenzymes NAD or NADP as the acceptor. X-ray crystallographic analysis shows that the coenzyme fits in a pocket made by the folding of the polypeptide chain. Many such enzymes combine specifically with **blue agarose** owing to putative structural similarity of the bound dye (Reactive Blue 2) to the coenzyme, a property that can be exploited in the separation and purification of these enzymes by affinity chromatography.

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A similar property is shown by some other nucleotide-binding enzymes (and also by certain other proteins that do not bind nucleotides).

nucleotide coenzyme any **nucleotide** (def. 2, 3) that is either (1) a coenzyme (e.g. nicotinamide-adenine dinucleotide), or (2) a substrate-carrier in an anabolic reaction (e.g. uridine diphosphate glucose).

nucleotide-gated channel *see* **ion channel**.

nucleotide reductase *see* **nucleoside diphosphate reductase, nucleoside triphosphate reductase**.

nucleotide sugar *an alternative name for* **nucleoside diphosphate sugar**.

nucleotide unit the repeating unit of a polynucleotide chain, defined typically by the sequence of atoms from the phosphorus atom at the 5′ end of any one of its component glycose residues to the oxygen atom at the 3′ end of the same residue and including all the atoms of the glycose residue and its attached phosphoric residue and nucleobase; atypically, the nucleotide unit at the 5′ end of a chain may lack a phosphate group. Nucleotide units in a given chain are numbered sequentially from the chain's 5′ end irrespective of the presence or absence of a phosphate group on the 5′-terminal unit.

nucleotidyl *the acyl group formed from a nucleoside* [mono]phosphate by removal of a hydroxyl group from its phosphoric group.

nucleotidyltransferase an enzyme of subclass EC 2.7.7; such enzymes transfer a nucleotidyl group to a reactant. Possession of such activity is a common mechanism of drug resistance (especially to **aminoglycoside antibiotics**) in bacteria. An example is gentamicin 2″-nucleotidyltransferase (EC 2.7.7.46); *systematic name*: NTP:gentamicin 2″-nucleotidyltransferase; *other name*: 2″-aminoglycoside nucleotidyltransferase. It catalyses a reaction between NTP and gentamicin to form pyrophosphate and 2″-nucleotidylgentamicin. This enzyme can be isolated from *Escherichia coli* and *Klebsiella pneumoniae* plasmids, and confers resistance to kanamycin, gentamicin, dibekacin, sisomicin, neomycin, and tobramycin by adenylating the 2″-OH group of these antibiotics. Example from *E. coli*: database code AADB_ECOLI, 177 amino acids (19.85 kDa).

nucleus (*pl.* **nuclei**) **1** *(in biology)* the most conspicuous organelle of a eukaryotic cell; it contains the chromosomes and (except for some activity in mitochondria) is the sole site of DNA replication and of RNA synthesis in the cell. Usually a spheroidal body, it is separated from the cytoplasm by the nuclear envelope. **2** *(in physics)* **atomic nucleus** the positively charged central part of an atom, with which is associated almost the whole of the mass of the atom but only a very small part of its volume. It is composed of nucleons, i.e. protons and neutrons. **3** *(in organic chemistry)* a characteristic arrangement of atoms, especially a ring structure, that occurs in a series of related organic compounds; e.g. the benzene nucleus. **4** a particle on which a crystal, droplet, or bubble forms in a fluid.

nuclide any individual species of atom, whether stable, metastable, or unstable, that is characterized by the constitution of its nucleus and by its **nucleon number**, **proton number**, and nuclear energy state; its mean life must be long enough for the species to be observable. Nuclides having the same proton number but different nucleon numbers or different nuclear energy states are termed isotopic nuclides, or **isotopes**. Nuclides having the same nucleon number but different proton numbers are termed isobaric nuclides, or **isobars**. Nuclides having the same neutron number but different proton numbers are termed isotonic nuclides, or **isotones**. A given nuclide may be specified by attaching its nucleon number either to the name of the relevant chemical element as a suffix, or to the symbol for the chemical element as a left superscript; the proton number may be attached to the symbol as a left subscript; e.g. carbon-14, ^{14}C, or $^{14}_{6}$C. A metastable nuclide (i.e. one with an elevated nuclear energy state) may be differentiated from its counterpart with the same nucleon number by attaching the suffix m to the nucleon number; e.g. technetium-99m or $^{99m}_{43}$Tc. (Absence of a nucleon number attached to its name or symbol implies the presence of all isotopes of the element in natural abundance.) —**nuclidic** *adj.*

nude a mutant strain of mouse or rat that lacks a **thymus gland** and hence is devoid of **T lymphocytes**. A linked locus also produces hairlessness, hence the name.

NUF1 *abbr. for* nuclear filament-related protein.

Nujol *a proprietary name for* a high-boiling-point fraction of liquid paraffin widely used for making mulls for infrared spectroscopy. It is also used medicinally as a laxative, and was referred to by the poet e. e. cummings in *Poem, or Beauty Hurts Mr. Vinal*: '...little liver pill-/hearted-Nujol-needing-There's-A-Reason...'.

null a minimum or zero value, especially of an electric current.

null cell *an alternative term for* **null lymphocyte**.

nullisomic **1** describing a cell, organism, strain, etc. that lacks one or more pairs of homologous chromosomes. **2** such a cell, organism, strain, etc.

null lymphocyte *or* **null cell** a **lymphocyte** that is not recognizable as either a B lymphocyte or a T lymphocyte.

null method *or* **zero method** a method of measurement in which a zero reading in a sensitive, but not necessarily calibrated instrument, e.g. a galvanometer, enables an unknown value of some property to be deduced by comparison with reference values.

NuMA *abbr. for* nuclear mitotic apparatus protein.

numatrin *another name for* **nucleolar phosphoprotein B23**.

number **1** a concept or expression of quantity reckoned in ones or units; a particular value of such a quantity (which may be integral or zero). **2** the symbol or group of symbols used to represent a number (def. 1); numeral; figure. **3** a numeral or string of numerals used for identification (of something, especially a member of a sequence). **4** to assign numbers to (members of a series); to label with a number or numbers.

number-average molar mass *see* **average molar mass**.

number-average relative molecular mass *or (formerly)* **number-average molecular weight** *see* **average relative molecular mass**.

number concentration *symbol*: C; *see* **concentration** (def. 1d).

number fraction *symbol*: δ; the number of defined particles or elementary entities of a specified component of a system divided by the total number of defined particles in the system.

numerical aperture *(in optics) abbr.*: NA; the arithmetic product of the refractive index of the medium in which the objective (lens) of a microscope is situated and the sine of half the angle of view of the objective. The resolving power of the lens is proportional to its numerical aperture.

nurse cell a cell that is connected by cytoplasmic bridges to an oocyte and thereby conveys macromolecules to the growing oocyte.

nus any of three *Escherichia coli* genes that are involved in transcriptional termination. Their gene products are as follows. NusA is a protein that binds to RNA polymerase, RNA, **rho**, and the antitermination protein pN, the product of the *N* gene. It may also bind to NusB. It participates in both the termination and antitermination of transcription. Database code NUSA_ECOLI, 495 amino acids (54.81 kDa). NusB is involved in the transcription termination process at certain sites during normal bacterial growth and is essential for the function of pN. Database code NUSB_ECOLI, 139 amino acids (15.67 kDa). NusG is involved in transcription antitermination. Database code NUSG_ECOLI, 181 amino acids (20.51 kDa).

NutraSweet *a proprietary name for* **aspartame**.

nutrient **1** any chemical substance that can be used by an organism to sustain its metabolic activities. **2** serving as or conveying nourishment. **3** *(in microbiology)* describing a solid or liquid medium that is able to support the growth of a range of nutritionally undemanding chemoorganotrophs.

nutrition **1** the supply of substances (i.e. nutrients) required by

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an organism, directly or indirectly, for its metabolic activities, i.e. for the provision of energy, for growth, and/or for the renewal of degraded components. **2** the act or process of supplying or receiving nutrients. **3** the scientific study of the nutrient requirements of particular organisms and of the supply of those nutrients. —**nutritional** *adj.*

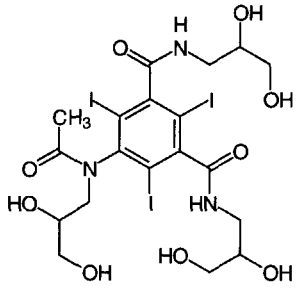
nutritional mutant a mutant strain of a microorganism (alga, bacterium, or fungus) that requires a supply of one or more growth factors in addition to those required by the wild type, i.e. a mutation in a **prototroph** to form an **autotroph**.

nutritive **1** containing nutrient(s). **2** of, concerned in, or promoting nutrition.

nux vomica the dried seeds of the Indian tree, *Strychnos nux-vomica*. They are a source of **strychnine**, **brucine**, and other poisonous alkaloids.

Nva *symbol for* the α-amino acid **norvaline** (now known as 2-aminovaleric acid, *symbol*: Avl).

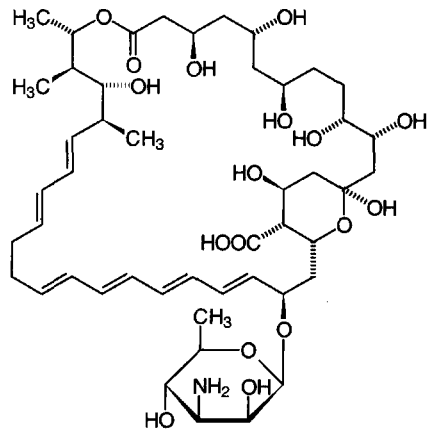
Nycodenz *the proprietary name for* *N*,*N*′-bis(2,3-dihydroxypropyl)-5-[*N*-(2,3-dihydroxypropyl)acetamido]-2,4,6-triiodoisophthalamide; a dense, synthetic, nonionic substance, highly soluble in water, that is capable of forming (autoclavable) aqueous solutions of densities up to 2.1 g mL^{-1}. It is one of several synthetic water-soluble triiodobenzene derivatives designed for use as intensifiers in radiology that have found use in isopycnic gradient fractionation of biological particles.



nyctalopia *the medical term for* **night blindness**.

nylon any of a class of synthetic thermoplastic substances, characterized chemically as long-chain polyamides and formed by condensation polymerization of dicarboxylic acids with diamines. They have high melting points, are insoluble, tough, resistant to fracture, and exhibit low friction. Hence they are useful in the manufacture of laboratory apparatus for which these properties are advantageous. Nylon can be formed into fibres or sheets and used for coatings, fabrics, and many other products. It is also used as an alternative to nitrocellulose in hybridization membranes.

nystatin a **mycosamine**-containing polyene antifungal antibiotic complex (three components) produced by *Streptomyces noursei* and other *Streptomyces* spp. It is very similar to **amphotericin B** in its properties and mechanism. Two proprietary names are Fungicidin and Mycostatin.



nystatin A_1

nystatin A_1

NZO mouse *abbr. for* New Zealand obese mouse.

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Oo

o+ *prefix (in peptide hormone nomenclature)* denoting ovine.

o- *prefix (in chemical nomenclature)* denoting ***ortho-***. *Compare* ***m-***, ***p-***.

O *symbol for* **1** oxygen. **2** a residue of the ribonucleoside orotidine (alternative to Ord).

O- *prefix (in chemical nomenclature)* indicating substitution on oxygen; a particular oxygen atom in a molecule may be specified by suffixing an appropriate superscript.

OA *abbr. for* ovalbumin.

OAA *abbr. for* oxaloacetic acid, or oxaloacetate.

OAG *abbr. for* 1-oleoyl-2-acetyl-glycerol.

Oakley–Fulthorpe technique a simple double immunodiffusion method that can be used for quantitative determination of antigen concentrations; it is essentially a development of the **Oudin technique**. As originally described, the antiserum in 1% agar is placed at the bottom of a cylindrical tube above which is placed a layer of 1% agar gel in 1% saline, and 0.5% *o*-cresol (as a preservative). Subsequently a bacterial filtrate (containing antigen) is layered onto the agar–saline gel and the tube then incubated at 37 °C. Disks or lines of flocculation of antigen–antibody complexes are produced in the agar–saline gel, from whose positions the concentration of antigen(s) may be determined. [After C. L. Oakley and A. J. Fulthorpe, who described the technique in 1953.]

O antigen **1** any of the lipopolysaccharide–protein somatic antigens of the cell walls of Gram-negative bacteria, especially those of the Enterobacteriaceae. They are useful in the serological classification of *Salmonella*, *Shigella*, and other bacteria. **2** *(sometimes) an alternative name for* H antigen (present on erythrocytes of blood group O); *see* **blood-group substance**.

ob *see* ***ob/ob***.

obelin a luminescent protein that is obtained from the jellyfish *Obelia geniculata*. It is similar to **aequorin** in properties and use.

obese having an excessive amount of body fat. —**obesity** *n.*

objective *(in optics)* the lens or system of lenses in an optical instrument (especially a compound microscope) that is positioned nearest to the object to be viewed.

oblate **1** having an equatorial diameter longer than the polar diameter. **2** describing an **ellipsoid of rotation** (including a spheroid) generated by rotation of an ellipse about its minor axis. **3** describing any protein of **oblate** (def. 1) dimensions as observed in hydrodynamic measurements. *Compare* **prolate**.

obligate by necessity, or without option; used especially of the nature of the environment or of the mode of life of an organism; e.g. obligate aerobe (*see* **aerobe**), obligate anaerobe (*see* **anaerobe**). *Compare* **facultative**.

O blood-group substance *see* **ABO system**.

ob/ob *the genotype symbol for* any of a number of strains of mouse with an inherited form of severe obesity, due to a homozygous recessive autosomal mutation on chromosome 6. Such animals display marked hyperglycemia and insulin resistance. A protein named **leptin**, or OB protein, has been implicated in the control of fat mass and is a product of the *ob* mutant gene, being deficient in *ob/ob* mice.

obtuse angle any plane angle greater than 0.5π rad or 90° and less than π rad or 180°.

Oc *symbol for* the octyl group.

Occam's razor *a variant spelling of* **Ockham's razor**.

occlude **1** to block or obstruct (a passage, tube, opening, etc.). **2** *(in chemistry)* to take up and retain something in the interstices of a solid; e.g. to absorb a gas into a metal or to entrap liquid within crystals during their formation. —**occlusion** *n.*

occludin an integral membrane protein that localizes in tight junctions in chick liver. There are four putative membrane-spanning segments within the N-terminal half. Example from chick: database code A49467, 504 amino acids (55.80 kDa).

occult concealed or hidden; not apparent to the unaided eye.

occult blood blood that is present in a sample in such small quantities, e.g. in feces, that it can only be detected by chemical testing or by microscopy.

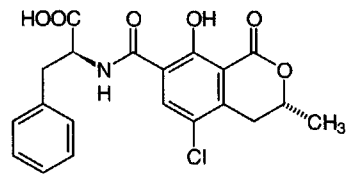
occult virus a virus whose presence in a host is inferred but whose isolation or detection cannot be achieved.

occupancy **1** the state or condition of being filled or occupied. **2** the number of similar sites occupied, usually expressed as a fraction or percentage of the total number available. It can refer, e.g., to the number of receptors on a cell surface occupied by a particular agonist or to the number of atomic orbitals of a particular subshell filled by electrons.

occupation theory of agonist action a theory stating that the magnitude of the response to an agonist is directly proportional to the fraction of specific receptors occupied by molecules of the agonist; it assumes that the binding of agonist to receptor is reversible. According to this theory the response will increase to a maximal value when all the receptors are occupied. *Compare* **rate theory of agonist action**.

Ochoa, Severo (1905–93), Spanish-born US biochemist; Nobel Laureate in Physiology or Medicine (1959) jointly with A. Kornberg 'for their discovery of the mechanisms in the biological synthesis of ribonucleic acid and deoxiribonucleic [sic] acid'.

ochratoxin any one of several **mycotoxins** produced by the fungus *Aspergillus ochraceous*, other *Aspergillus* spp., and *Penicillium* spp.; the major component, ochratoxin A, is a complex, chlorine-containing derivative of L-phenylalanine that inhibits phosphoenolpyruvate carboxykinase (EC 4.1.1.49). These toxins may occur on contaminated foodstuffs such as corn (maize), peanuts, storage grains, etc.



ochratoxin A

ochre codon or **ochre triplet** *symbol*: UAA; one of the three terminator codons or **nonsense codons** found in messenger RNA.

ochre mutant any cell or virus carrying an **ochre mutation**.

ochre mutation a mutation that gives rise to an **ochre codon** at an abnormal position in a messenger RNA molecule.

ochre suppressor any of a number of mutations, occurring in *Escherichia coli*, that suppress an **ochre codon** in messenger RNA thereby allowing insertion of one of several alternative amino acids into a polypeptide chain at that site. The mutation results in changed anticodons of the transfer RNA molecules, consequent on single-base substitution in their DNA coding sequences. Ochre suppressors also suppress **amber codons**.

ochronosis the presence of brown-black pigment in the skin, cartilage, and other tissues due to **alcaptonuria**.

Ockham's razor *or* **Occam's razor** a maxim stating that when explaining something there should be a minimal number of assumptions. *Entia non sunt multiplicanda praeter necessitatem* (entities should not be multiplied except from necessity). [After William of Ockham (1285–1349), English philosopher.]

Oco *symbol for* the octanoyl group.

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OCS *the proprietary name for* a commercial xylene–fluor mixture suited to the liquid-scintillation counting of a wide range of toluene- and xylene-soluble organic samples, especially specimens solubilized in **NCS**.

oct+ *a variant form of* **octa+** (sometimes before a vowel).

OCT *(in clinical chemistry) abbr. for* ornithine carbamoyltransferase.

OCT a family of genes encoding transcription factors for eukaryotic RNA polymerase II promoters. The proteins contain a **POU domain** and contribute to the naming of that domain. They are leucine zipper proteins and bind to **octamer** sequences. Examples from human: Oct-1, a factor for snRNA and histones: database code OCT1_HUMAN, 743 amino acids (76.40 kDa); Oct 2, a factor for immunoglobulin promoters: database code OCT2_HUMAN, 478 amino acids (51.02 kDa).

octa+ *or* **octo+** *or (sometimes before a vowel)* **oct+** *comb. form* denoting eight, eightfold, eight times.

octacosa+ *comb. form* denoting twenty-eight, twenty-eightfold, twenty-eight times.

octacosanoate *see* **montanate**.

octacosanoyl *see* **montanoyl**.

octadeca+ *comb. form* denoting eighteen, eighteenfold, eighteen times.

octadecadienoic acid any straight-chain fatty acid having eighteen carbon atoms and two double bonds per molecule. Linoleic acid (*see* **linoleate**) is the *all-Z*-(9,12)-isomer and is a constituent of most vegetable oils and animal fats. The *all-E*-isomer of this acid is linolelaidic acid, a constituent of the seeds of *Chilopsis linearis*, which also contain the *all-E*-(10,12)-isomer. A number of other isomers have been synthesized chemically.

octadecanoic acid *the systematic name for* stearic acid; *see* **stearate**.

octadecapentaenoic acid any straight-chain fatty acid having eighteen carbon atoms and five double bonds per molecule. The *all-Z*-(3,6,9,12,15)-isomer occurs naturally in dinoflagellates.

octadecatetraenoic acid any straight-chain fatty acid having eighteen carbon atoms and four double bonds per molecule. Several isomers occur naturally, including the 3*E*,9*Z*,12*Z*,15*Z*-isomer, found in seed oil, and the *all-Z*-(6,9,12,15)-isomer, found in fish oil. The 9*Z*,11*E*,13*E*,15*Z*-isomer and the *all-E*-(9,11,13,15)-isomer are α- and β-parinaric acid respectively, from *Parinarium laurinum*; both isomers are used as fluorescent probes.

octadecatrienoic acid any straight-chain fatty acid having eighteen carbon atoms and three double bonds per molecule. A number of isomers occur naturally, the most prominent being the *all-Z*-(9,12,15)-isomer, (9,12,15)-linolenic acid; the *all-Z*-(6,9,12)-isomer is (6,9,12)-linolenic acid (*see* **linolenate**). *See also* **columbinic acid**, **eleostearate**.

octadecenoic acid any straight-chain fatty acid having eighteen carbon atoms and one double bond per molecule. (*Z*)-Octadec-9-enoic acid (i.e. oleic acid; *see* **oleate**) is the isomer found widely, often in high proportion, in plant and animal lipids, especially in olive oil. The 5*E*- and 6*Z*-(petroselenic acid; *see* **petroselenate**) isomers are found in seed oils; the 6*E*- isomer is named **petroselaidic acid**, and the 9*E*- isomer is elaidic acid, a common constituent of fats and oils (*see* **elaidate**). The 11*E*- and 11*Z*-isomers are, respectively, *trans*- and *cis*-vaccenic acid (*see* **vaccenate**).

octaethyleneglycol mono-*n*-decyl ether a nonionic $C_{10}E_8$ detergent (*see* C_xE_y).

octaethyleneglycol mono-*n*-dodecyl ether a nonionic $C_{12}E_8$ detergent (*see* C_xE_y).

octahedral coordination coordination in which six ligands are disposed about a central atom as if at the vertices of an octahedron enclosing that atom.

octahedron (*pl.* **octahedra**) any solid geometrical figure having eight plane triangular faces, 12 edges, and six tetrameric vertices. In a regular octahedron the faces are congruent equilateral triangles and may be considered to consist of two equal pyramids opposing each other on the same square base. —**octahedral** *adj.*

octamer **1** an eight-base sequence element that is common in eukaryotic **promoters**. The consensus sequence is ATTTGCAT. It binds a number of transcription factors (*see* ***OCT***). **2** any polymer of a protein having eight subunits, e.g. β-lactoglobulin at pH 4.7 below 4°C. **3** an assembly of eight **histones** containing two each of H2A, H2B, H3, and H4, that forms the histone core of the nucleosome.

octanoate *or (formerly)* **caprylate** **1** *systematic and preferred name for* the anion, CH_3–$[CH_2]_6$–COO^-, derived from octanoic acid (formerly known as caprylic acid) . **2** any mixture of octanoic acid and its anion. **3** any salt or ester of octanoic acid.

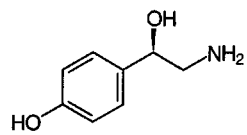
octanoyl *or (formerly)* **capryloyl** *or* **caprylyl** *symbol*: Oco; the univalent acyl group, CH_3–$[CH_2]_6$–CO–, derived from octanoic acid (formerly known as caprylic acid).

octet **1** any group of eight. **2** *(in chemistry)* (esp. valency) a stable group of eight electrons constituting an electron shell of an atom.

octo+ *a variant form of* **octa+**.

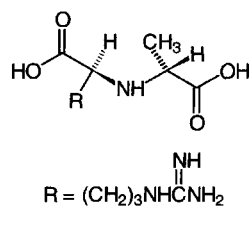
octonic acid any monocarboxylic **aldonic** acid formally derived from an octose by oxidation at C-1.

octopamine β-hydroxytyramine; 1-(*p*-hydroxyphenyl)-2-aminoethanol; the D(–)-enantiomer is a biogenic amine, about one-tenth as active as norepinephrine, formed by the β-hydroxylation of tyramine by dopamine β-hydroxylase. It is found in the salivary glands of *Octopus* spp. and of *Eledone moschata*.



R-(–)-enantiomer

octopine **1** *N*-(1-carboxy-4-guanidinobutyl)-L-alanine; N^2-(1-carboxyethyl)-L-arginine; D-octopine (i.e. N^2-(D-1-carboxyethyl)-L-arginine) is an **opine** found in the tumours of crown-gall disease in plants and in the muscles of certain invertebrates. The genes responsible for the synthesis of octopine are part of the **T-DNA** from a **Ti-plasmid**. **2** any opine that, like octopine itself, is an *N*-substituted derivative of alanine. Octopine was first isolated from the muscles of *Octopus*, but is found in other cephalopod species and lamellibranchs. The guanidine group can undergo phosphorylation to phosphooctopine, which acts as a **phosphagen**. *Compare* **octopinic acid**.



D-octopine

octopinic acid *N*-(1-carboxy-4-aminobutyl)-L-alanine; N^2-(1-carboxyethyl)-L-ornithine; D-octopinic acid (i.e.N^2-(D-1-carboxyethyl)-L-ornithine) is an **opine** found in the tumours of crown-gall disease of plants; it is a member of the **octopine** (def. 2) family.

octose any **aldose** having a chain of eight carbon atoms in the molecule.

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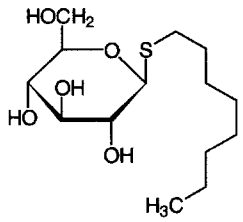
octulose any **ketose** having a chain of eight carbon atoms in the molecule.

octyl *symbol*: Oc; the alkyl group, CH_3–$[CH_2]_6$–CH_2–, derived from octane.

octyl glucoside *n*-octyl β-D-glucopyranoside; a mild nonionic detergent, aggregation number 84, CMC 20–25 mM. The α-glucoside isomer has also been used, e.g. for crystallization of membrane proteins. The lack of absorbance at 228 nm is an advantage in the use of these compounds. *Compare* **heptyl glucoside**, **hexyl glucoside**, **nonyl glucoside**, **octyl maltoside**.

octyl maltoside *n*-octyl β-D-maltopyranoside; a mild nonionic detergent, CMC 23 mM. *Compare* **octyl glucoside**.

octyl thioglucoside *n*-octyl 1-thio-β-D-glucopyranoside; a mild nonionic detergent, CMC 9 mM, with properties similar to other alkyl glucosides.



ocular **1** of or concerned with the eye or vision. **2** *or* **eyepiece** the lens or system of lenses in an optical instrument (especially a compound microscope) that is positioned nearest to the eye.

ocytocin *(sometimes) a variant spelling of* **oxytocin**.

od *or* **o.d.** *abbr. for* outside diameter.

OD *or* **O.D.** *abbr. for* optical density (now called **absorbance**).

Oe *symbol for* oersted.

oedema *an alternative spelling (esp. Brit.) of* **edema**.

oenanthate *an alternative spelling (esp. Brit.) of* enanthate (*see* **heptanoate**).

oenology *an alternative spelling (esp. Brit.) of* **enology**.

oersted *symbol*: Oe; the cgs unit of magnetizing force or magnetic field strength;

1 oersted = $10^3/4\pi$ amperes per metre (= 79.58 A m^{-1}).

[After Hans Christian Oersted (1777–1851), Danish physicist and chemist who discovered the phenomenon of electromagnetism.]

17β-oestradiol *an alternative spelling (esp. Brit.) of* **17β-estradiol**.

OEt *symbol for* the ethoxy group, CH_3–CH_2–O– (alternative to EtO).

off-rate the constant, k_{-1}, for the dissociation step in any binding equilibrium, e.g. LB → L + B in the equilibrium L + B = LB, where L represents ligand and B the molecule it binds; the rate of dissociation of a ligand from the bound complex. The dimensions of k_{-1} are $time^{-1}$. *Compare* **dissociation constant**, **on-rate**.

OGCP *abbr. for* oxoglutarate/malate carrier protein; a mitochondrial inner membrane integral protein that plays an important role in several processes, including the malate–aspartate shuttle, gluconeogenesis from lactate, and nitrogen metabolism. Example from human: database code M2OM_HUMAN, 313 amino acids (33.91 kDa). *See also* **mitochondrial carrier proteins**.

+ogen *a variant form of* **+gen** (after a consonant).

Ogston concept *or* **three-point attachment hypothesis** a concept formulated to explain the inherent differing reactivities, often expressed in an enzymic reaction, of identical chemical groups in a **prochiral** molecule. It states that there must be at least three points of attachment of a substrate molecule to the active site of an enzyme. It is similar to the **Easson–Stedman model**. [After Alexander George Ogston (1911–96), British biophysicist who formulated it in 1948.]

25-OHD$_3$ *abbr. for* 25-hydroxycholecalciferol; calcidiol; use not recommended.

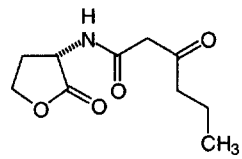
1,25-(OH)$_2$D$_3$ *abbr. for* 1,25-dihydroxycholecalciferol; **calcitriol**; use not recommended.

24,25-(OH)$_2$D$_3$ *abbr. for* 24(*R*),25-dihydroxycholecalciferol; (24*R*)-hydroxycalcidiol; use not recommended.

25,26-(OH)$_2$D$_3$ *abbr. for* 25,26-dihydroxycholecalciferol; 26-hydroxycalcidiol; use not recommended.

1,24,25-(OH)$_3$D$_3$ *abbr. for* 1,24(*R*),25-trihydroxycholecalciferol; **calcitetrol**; use not recommended.

OHHL *abbr. for N*-(3-oxohexanoyl)-L-homoserine lactone.



ohm *symbol*: Ω; the SI derived unit of electric resistance, defined as the resistance between two points on a conductor through which a current of one ampere flows as the result of a potential difference of one volt applied between the points, the conductor not being the source of any electromotive force; i.e. 1 Ω = 1 V A^{-1}. [After Georg Simon Ohm (1787–1854), German physicist.]

Ohm's law a law stating that under constant conditions the current, *I*, flowing through a given conductor is proportional to the potential difference, *U*, applied across it. The law is often expressed in the form $U = IR$, where the proportionality constant, *R*, is the resistance of the conductor.

+oic *suffix (in chemical nomenclature)* denoting the carboxyl group, –COOH. It is added to the systematic name of an unbranched alkane (or substituted alkane) to denote its modification to the corresponding alkanoic (i.e. carboxylic) acid by formal conversion of a methyl group to a carboxy group; e.g. hexanoic acid, CH_3–$[CH_2]_4$–COOH, formally derived from hexane, CH_3–$[CH_2]_4$–CH_3. It is used also in the trivial names of certain carbocyclic and heterocyclic carboxylic acids; e.g. benzoic acid, furoic acid.

+oid *suffix forming adjectives and (associated) nouns* **1** denoting likeness to, or having the form of (something specified); e.g. colloid (i.e. gluelike substance). **2** generated by rotation of (the geometrical figure specified); e.g. ellipsoid (i.e. solid figure derived from an ellipse). **3** belonging to the class or group represented by (the type member specified); e.g. steroid (i.e. compound belonging to the same chemical family as sterols). —**+oidal** *adj.*

oil any of a large, heterogeneous group of neutral, flammable substances that are liquid at room temperature and are characteristically soluble in relatively nonpolar solvents but only sparingly soluble in aqueous solvents. There are three main distinctive groups: (1) animal and vegetable oils, which usually consist predominantly of triacylglycerols but may contain varying amounts of fatty-acid esters of other alcohols; (2) mineral oils, derived from petroleum, coal, shale, etc., which consist predominantly of hydrocarbons; and (3) **essential oils**.

oil body *an alternative name for* **spherosome**.

oil-immersion objective an objective lens in a light microscope designed to be used with a layer of a special oil between the object (or its coverslip) and the lens. The oil is of the same refractive index as the glass of the lens. This arrangement maximizes the numerical aperture and hence the resolving power of the lens.

Oil Red O a stain for lipid it is widely used for staining lipoproteins on cellulose acetate electrophoretic strips.

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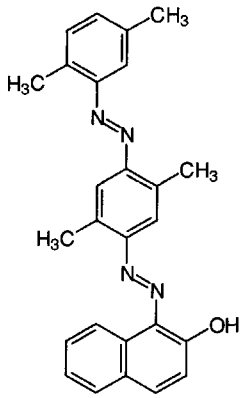


Oil Red O

oilseed rape *or* **colza** *the common name for Brassica campestris*, a species of rape grown as a source of rapeseed oil.

okadaic acid a polyether fatty acid, M_r = 804.9, used as a potent inhibitor of **protein phosphatases**, especially the PP-1 and PP-2A types. It does not inhibit protein tyrosine kinases and does not activate protein kinase C. It is a tumour promoter, and is implicated as the causative agent of diarrhetic shellfish poisoning. Its name derives from *Hilichondria okadaii*, a marine sponge that feeds on *Prorocentrum lima*, a dinoflagellate from which it is isolated. See structure below.

Okazaki fragment *or* **Okazaki piece** *or* **Okazaki segment** any of the relatively short polydeoxyribonucleotides that are formed, concomitantly with the continuous replication of one of the two strands of a duplex DNA molecule, as intermediates during the discontinuous replication of the other strand. Such fragments are synthesized from mononucleotides in a direction opposite to that of the movement of the replication fork; then, as replication proceeds, they are covalently joined through the action of a polynucleotide ligase to form a long daughter polynucleotide chain, the lagging strand. These fragments appear to be 1000–2000 residues long in *Escherichia coli* and 100–200 residues long in mammalian cells; a proportion of them may have RNA primer attached. [After Reiji Okazaki (1930–1975), Japanese molecular biologist.]

OK cell *abbr. for* opossum kidney cell; any cell of a culture derived from this organ and used to study α_{2C} adrenoceptors.

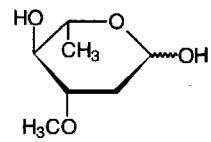
+ol *suffix (in chemical nomenclature)* indicating the presence of a hydroxyl group attached to a carbon atom.

+olate *suffix* used as an alternative to **+oxide** (def. 1).

old yellow enzyme *an obsolete name for* the enzyme NADPH dehydrogenase (EC 1.6.99.1), a yellow flavoprotein (FMN in yeast, FAD in plants). *Compare* **new yellow enzyme**.

Ole *symbol for* the oleoyl (i.e. (*Z*)-octaden-9-enoyl) group.

oleandrose 2,6-dideoxy-3-*O*-methyl-*arabino*-hexose; the L enantiomer is a component of some **cardiac glycosides**.



L-oleandrose

oleate **1** *numerical symbol*: 18:1(9); *the trivial name for Z*-octadec-9-enoate, CH_3–$[CH_2]_7$–CH=CH–$[CH_2]_7$–COO^- (*cis* isomer), the anion derived from oleic acid (i.e. *Z*-octadec-9-enoic acid), a monounsaturated straight-chain higher fatty acid. *See also* **octadecenoic acid**, **oleic family**. **2** any mixture of free oleic acid and its anion. **3** any salt or ester of oleic acid. *Compare* **elaidate**, **vaccenate**.

oleate desaturase *see* **phosphatidylcholine desaturase**.

olefin *an older name for* an alkene. —**olefinic** *adj.*

oleic family (of polyunsaturated fatty acids) a series of polyenoic acids in which the hydrocarbon chain terminates with the alkenyl grouping CH_3–$[CH_2]_7$–CH=CH– (as in oleic acid); there are three other series, i.e. the **linoleic family**, **linolenic family**, and **palmitoleic family**. The oleic family can be synthesized from acetyl-CoA: palmitoyl-CoA is first synthesized by the fatty-acid synthase (*see* **fatty-acid synthase complex**); next, by chain elongation and action of **desaturases**, stearoyl-CoA, oleoyl-CoA, and longer chain fatty acyl-CoA compounds are synthesized; then from their respective CoA derivatives, the cognate fatty acids are formed. The series includes (*all-Z*)-eicosa-5,8,11-trienoic acid. In **essential fatty acid deficiency** in mammals, longer chain polyunsaturated fatty acids of the oleic family are synthesized, and partially substitute for long-chain polyunsaturated fatty acids of the linoleic family. *See also* **eicosenoic acid**, **eicosatrienoic acid**, **Mead acid**.

olein *an old name for* any of the glyceryl esters of oleic acid (*see* **oleate**), especially the triester, **triolein** (i.e. trioleoylglycerol).

oleo *(US) abbr. for* oleomargarine.

oleomargarine *an alternative name (esp. US) for* **margarine**.

oleosome *an alternative name for* **spherosome**.

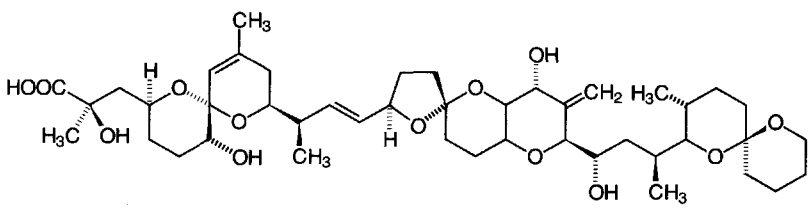
oleoyl *or (formerly)* **oleyl** *symbol*: Ole; *the trivial name for* (*Z*)-octadec-9-enoyl, CH_3–$[CH_2]_7$–CH=CH–$[CH_2]_7$–CO– (*cis* isomer), the acyl group derived from oleic acid (i.e. (*Z*)-octadec-9-enoic acid). It occurs very widely in natural lipids. *Compare* **elaidoyl**, **vaccenoyl**. *See also* **oleic family**.

1-oleoyl-2-acetylglycerol *abbr.*: OAG; an activator of protein kinase C.

oleum fuming sulfuric acid; a solution of SO_3 in concentrated $H_2SO_4 \rightarrow H_2S_2O_7$.

oleyl **1** *a common name for Z*-octadec-9-enyl, CH_3–$[CH_2]_7$–CH=CH–$[CH_2]_8$– (*cis* isomer), the monoalkenyl group derived from *Z*-octadec-9-ene; use deprecated. **2** *an old and misleading trivial name for Z*-octadec-9-enoyl; oleoyl now used.

olfactomedin a major glycoprotein component of the extracellular matrix of olfactory neuroepithelium. Example (precursor) from *Rana catesbeiana*: database code OLFM_RANCA, 464 amino acids (52.51 kDa).



okadaic acid

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olfactory receptor any of a group of integral membrane proteins thought to be involved in effecting the sense of smell. They are similar to other G-protein-coupled receptors; several are known (or suspected). Example, presumed olfactory receptor-like protein HGMP07E from human: database code OLFE_HUMAN, 312 amino acids (35.17 kDa); five motifs.

+olide *suffix* (to the chemical name of an aliphatic hydrocarbon) denoting conversion to a lactone having the same number of carbon atoms as the parent hydrocarbon.

oligo *abbr. (colloquial) for* **oligonucleotide**.

oligo+ *or (before a vowel)* **olig+** *comb form* denoting **1** few, little, not much, or not many. **2** *(in chemistry and biochemistry)* a small number of (the component specified); e.g. **oligopeptide**. **3** *(in pathology)* deficiency or insufficiency of (some thing or some attribute); e.g. **oliguria**. *Compare* **multi+**, **poly+**.

oligo-2′,5′-adenylate synthetase an enzyme of the sub-subclass EC 2.7.7 that binds double-stranded RNA and polymerizes ATP into pppA(2′p5′A)$_n$ oligomers; the latter activate the latent RNase L causing it to cleave single-stranded RNAs. The enzyme is induced by **interferons**. It is a homotetramer, associated with many different subcellular fractions. In humans, two forms, E16 and E18, are produced by alternative splicing of the same gene. Examples from human, E16: database code 25A1_HUMAN, 364 amino acids (41.73 kDa); E18: database code 25A2_HUMAN, 400 amino acids (46.00 kDa).

oligodendrocyte a type of glial cell that forms and supports the myelin sheath around axons in the central nervous system of vertebrates. In contrast to the **Schwann cell**, which performs this role in peripheral neurons for a single axon, one oligodendrocyte is involved in the myelination of several axons.

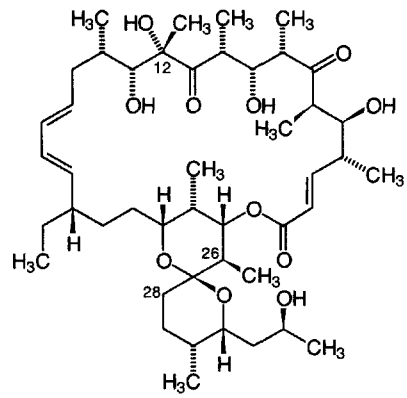
oligo-1,6-glucosidase (EC 3.2.1.10), *other names*: sucrase-isomaltase; limit dextrinase; isomaltase; an enzyme that catalyses the hydrolysis of 1,6-α-D-glucoside linkages in isomaltose and dextrins produced from starch and glycogen by α-amylase. Example, isomaltase from *Bacillus cereus*: database code O16G_BACCE, 558 amino acids (65.94 kDa). A similar enzyme is intestinal human enzyme, which has sucrase/maltase activity; EC 3.2.1.48): database code SUIS_HUMAN, 1827 amino acids (209.17 kDa).

oligohistidine the homopolypeptide of histidine; the term is used in referring to a **histidine tail**.

oligomer **1** *(in chemistry and biochemistry)* any substance or type of substance that is composed of molecules containing a small number – typically two to about ten – of constitutional units in repetitive covalent linkage; the units may be of one or of more than one species. Depending on the branch of chemistry concerned, an oligomer may or may not be considered to be a variety of **polymer**. **2** *(in molecular biology and enzymology)* any multimeric protein that contains a finite, relatively small, number of identical subunits (i.e. protomers) that are not in covalent linkage but in a state of reversible association with each other; the protomers may themselves each consist either of single polypeptide chains (i.e. monomers) or of two or more reversibly associated (identical or nonidentical) monomers. This definition is based exclusively on the identity of the subunits and does not restrict the number of polypeptide chains each identical subunit may contain. —**oligomeric** *adj.*; **oligomerize** *or* **oligomerise** *vb.*; **oligomerization** *or* **oligomerisation** *n.*

oligomycin any of a group of closely related **macrolide** antibiotics produced by an actinomycete similar to *Streptomyces diastatochromogenes*. Oligomycin B is an inhibitor of oxidative phosphorylation in mitochondria, interfering with the passage of hydrons through the F_0 component of **H$^+$-transporting ATP synthase**, and of photophosphorylation in chloroplasts. Oligomycin D (**rutamycin**) is useful as an antifungal agent. (Illustrated opposite.)

oligomycin sensitivity-conferring protein *abbr.*: OSCP; a protein component of mitochondrial ATP synthase that is required for the binding of the F_1 component to the F_0 component of the enzyme system. *See also* **H$^+$-transporting ATP synthase**.



oligomycin A
oligomycin B: 28-oxo
oligomycin C: 12-deoxy
oligomycin D: 26-demethyl

oligonucleotide *abbr. (colloquial)*: oligo; any molecule that contains a small number (two to about ten) of nucleotide units connected by phosphodiester linkages between (usually) the 3′ position on the glycose moiety of one nucleotide unit and the 5′ position on the glycose moiety of the adjacent one.

oligopeptide any molecule that contains a small number (2 to about 20) of amino-acid residues connected by peptide linkages.

oligophosphate **1** any ion or salt of an **oligophosphoric acid** — an acid containing commonly two or three, but sometimes four or more, phosphoric residues connected by anhydride linkages. **2** any mixture of a free oligophosphoric acid and its various anions. **3** *or* **oligophosphoric ester** any ester of an oligophosphoric acid.

oligosaccharide any molecule that contains a small number (2 to about 20) of monosaccharide residues connected by glycosidic linkages.

oligosaccharin any of a group of regulatory oligosaccharides, including a fungal heptaglucoside and a plant oligogalacturonide, that are released from cell walls and control functions such as growth, development, reproduction, and defence against disease. They also include xyloglucans.

***N*-oligosaccharyltransferase** an enzyme that transfers an oligosaccharide with high mannose content from a lipid-linked oligosaccharide donor to an asparagine acceptor site on newly synthesized glycoproteins. It has three subunits: **ribophorins** I and II, and a 48 kDa subunit, database code (precursor) OST4_HUMAN, 456 amino acids (50.71 kDa).

oligotrophic describing a habitat, especially a lake or other mass of water, that is poor in nutrients capable of supporting the growth of aerobic plants and microorganisms, and (in the case of a lake, etc.) that hence contains abundant dissolved dioxygen at all depths.

olivomycin one of several related components of a complex of antibiotics produced by *Streptomyces olivoreticuli*. It has been investigated for antineoplastic activity. It is used as a dye specific for G–C base pairs, and stains the R bands first demonstrated in Giemsa staining.

+oma (*pl.* **+omas** *or* **+omata**) *suffix* denoting a tumour.

OMe *symbol for* the methoxy group, CH_3–O– (alternative to MeO).

omega *symbol*: ω (lower case) *or* Ω (upper case); the twenty-fourth and last letter of the Greek alphabet. For uses *see* **Appendix A**.

Omega *an alternative name for* **Mega-8**.

omega-oxidation *or* **ω-oxidation** a minor oxidative metabolic pathway of fatty acids, particularly those of medium chain-length, in which the methyl group that contains the carbon atom furthest from the carboxyl group of such an acid is oxi-

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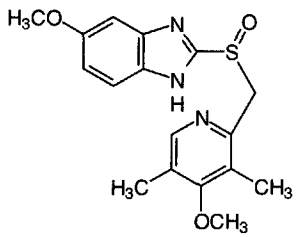
dized first to a hydroxymethyl group and ultimately to another carboxyl group.

omega protein *or* **ω-protein** *an alternative name for* type I **DNA topoisomerase**.

omeprazole *the nonproprietary pharmaceutical name for* 5-methoxy-2-{[(4-methoxy-3,5-dimethyl-2-pyridinyl)methyl]sulfinyl}-1*H*-benzimidazole, a gastric proton-pump inhibitor. It blocks both basal and stimulated secretion of acid in the stomach by reversibly inhibiting H^+/K^+-transporting ATPase (EC 3.6.1.36) in the cell membranes of parietal cells within the oxyntic glands of the gastric mucosa. It is useful clinically in the treatment of erosive reflux esophagitis, benign peptic ulcer, and Zollinger–Ellison syndrome. *Proprietary name*: Losec.



omicron *symbol*: o (lower case) *or* O (upper case); the fifteenth letter of the Greek alphabet.

ommatidium any of many identical structural units of the compound eye found in many invertebrates. In *Drosophila*, each consists of eight photoreceptor cells and 12 accessory cells. In sevenless and bride-of-sevenless mutants, one of the photoreceptor cells fails to develop.

ommatin a type of **ommochrome**.

ommatochrome *an alternative name for* **ommochrome**.

ommin a type of **ommochrome**.

ommochrome *or* **ommatochrome** any of a large group of yellow, brown, red, or violet natural polycyclic pigments especially commonly found in the Arthropoda, particularly in the ommatidia of the compound eye. They all contain a phenoxazine nucleus and are formed biologically from tryptophan via kynurenine. Ommochromes are divided into two groups: **ommatins**, which are alkali-labile, of low relative molecular mass, and rather weakly coloured; and **ommins**, which are alkali-stable, and of higher relative molecular mass and more strongly coloured than the ommatins.

OMP *abbr. for* orotidine monophosphate; *see* **orotidine phosphate**.

OMP decarboxylase *abbr. for* orotidine-5′-phosphate decarboxylase, a reaction carried out by the multifunctional enzyme **uridine 5′-monophosphate synthase**.

+onate *noun suffix* denoting the anion, a salt, or an ester of an aldonic acid. *See also* **uronate**.

onco+ *comb. form* denoting **1** tumour. **2** volume.

oncofetal parvalbumin *see* **oncomodulin**.

oncogen any agent that causes **oncogenesis**; the term embraces **carcinogen**.

oncogene any gene associated with the causation of cancer. The first oncogenes to be characterized were isolated from acutely transforming **retroviruses**; it was found subsequently that the retroviral oncogenes (v-*onc*) were related to, and probably derived from, normal cellular genes (c-*onc*), which came to be termed **protooncogenes**; these in most cases are involved with growth control. The derivation of oncogenes from protooncogenes is presumed to be the consequence of mutations in protooncogenes after capture by the virus, removing regulatory constraints from the protooncogene or its product. This may result from (1) deletions of portions of the oncogene; (2) mutation of the oncogene resulting in a protein product that is in an active state even in the absence of any normally required stimulus; (3) translocation of the gene from the normal site of expression, resulting in an altered gene product with aberrant function; or (4) amplification of the gene resulting in inappropriate expression or overexpression of the product. Protooncogenes function in normal cells in growth and differentiation pathways. They and their oncogenic counterparts can be grouped into categories based on their roles in these processes. Some have products that act as growth factors (e.g. *sis*, *int-2*) or growth-factor receptors (e.g. *fms*, *neu*, *kit*). Others encode signal-transduction molecules normally activated by growth-factor receptors (e.g. *ras*, *raf*, *mos*, and *src* family members). Others encode proteins that function in the nucleus (e.g. *myc*, *myb*, *fos*, *jun*) where they influence the expression of other genes. For further details see under individual oncogenes. Strictly speaking, those genes carried by DNA tumour viruses, such as **SV40** and **adenoviruses**, should also be construed as oncogenes. Unlike the retroviral genes, however, they appear to have no cellular counterparts but instead operate by subverting the actions of cellular genes (such as protooncogenes) that normally function to control cell growth. *See also* ***FMS***, ***FOS***, ***int-2***, ***JUN***, ***KIT***, ***MOS***, ***MYB***, ***MYC***, ***neu***, ***RAF***, ***RAS***, ***sis***, ***src***.

oncogenesis the production or formation of neoplastic tumours or a neoplastic tumour, whether benign or malignant; the term embraces **carcinogenesis**.

oncogenic (of an agent) causing the formation of a neoplastic tumour or tumours; of or pertaining to **oncogenesis**; the term embraces carcinogenic. —**oncogenicity** *n.*

oncology the branch of medicine concerned with the study and treatment of neoplastic tumours. —**oncological** *adj.*; **oncologist** *n.*

oncolysis the destruction of neoplastic tumours or tumour cells, whether spontaneous or in response to treatment. —**oncolytic** *adj.*

oncomodulin *other names*: parvalbumin beta; oncofetal parvalbumin; an **EF-hand** Ca^{2+}-binding protein that may function in a similar manner to **calmodulin**. Expression is limited to early embryonic stages, the placental cytotrophoblasts, and neoplastic tissues. Example from human: database code ONCO_HUMAN, 108 amino acids (12.01 kDa).

oncornavirus *an old name for* a group of RNA tumour viruses now classified in the subfamily Oncovirinae. *See* **retrovirus**.

oncostatin M *abbr.*: OSM; a polypeptide cytokine, produced by activated T cells and PMA-treated monocytes, that inhibits the growth of a variety of cancer cells, but stimulates growth of AIDS-Kaposi's sarcoma-derived cells and normal fibroblasts. It is a member of the **interleukin 6** subfamily. It exists as a monomer. Example from human (precursor): database code ONCM_HUMAN, 252 amino acids (28.48 kDa); residues 1–25 are the signal, 26–234 oncostatin M, and 235–252 a propeptide.

oncotic pressure the **colloid osmotic pressure** of plasma proteins; it is important as an index of the flow of water between the blood and the fluid in the tissues.

+one *noun suffix* denoting ketone.

one-carbon compound *an alternative name for* **C_1 compound**.

one cistron–one polypeptide hypothesis *an alternative name for* the **one gene–one polypeptide hypothesis**.

one gene–one antigen hypothesis a hypothesis stating that each of the genes in a tissue transplant governing the host's reaction to it is responsible for the manufacture of a particular transplantation antigen and for that antigen alone. It was first formulated by W. **Beadle** and E.L. **Tatum**.

one gene–one enzyme hypothesis a hypothesis, developed from the **one gene–one reaction hypothesis**, stating that every enzyme is synthesized under the control of a different individual gene. It was subsequently refined into the **one gene–one polypeptide hypothesis**.

one gene–one polypeptide hypothesis *or* **one cistron–one polypeptide hypothesis** a hypothesis stating that each naturally occurring polypeptide is synthesized biologically under the control of a different corresponding gene, which is transcribed into a unique species of messenger RNA specifying the polypeptide in question. Subsumed within this hypothesis are various earlier ones, formulated before the molecular basis of

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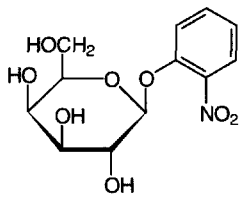
the genetic control of polypeptide synthesis had been elucidated.

one gene–one reaction hypothesis a hypothesis stating that every specific biochemical reaction is under the ultimate control of a different gene. It was later redefined as the **one gene–one enzyme hypothesis**.

+onic *suffix* denoting the formal conversion of an aldose to the corresponding aldonic acid; e.g. glucose gives rise to gluconic acid.

+onium *noun suffix* denoting a cationic molecular entity in which a heteroatom is bonded to one more univalent ligand than is normal for a neutral molecule containing that heteroatom and therefore bears a formal positive charge; e.g. ammonium, H_4N^+; dimethylammonium, $(CH_3)_2H_2N^+$; diphenyliodonium, $(C_6H_5)_2I^+$; trialkylsulfonium, R_3S^+ (where R = alkyl). *See also* **carbonium ion** (def. 2).

ONPG *abbr. for ortho*-nitrophenyl-β-D-galactopyranoside; a chromogenic substrate used for the detection and assay of β-galactosidase activity.



on-rate the constant, k_{+1}, for the association step L + B → LB in the equilibrium L + B = LB, where L represents ligand and B the molecule it binds; the rate of association of ligand to form a complex. The dimensions of k_{+1} are time^{-1}. *Compare* **association constant**, **off-rate**.

Onsager, Lars (1903–76), Norwegian-born US physical chemist noted for his work on the theory of dielectrics and for his research into nonequilibrium thermodynamics; Nobel Laureate in Chemistry (1968) for 'the discovery of the reciprocal relations bearing his name, which are fundamental for the thermodynamics of irreversible processes'.

Onsager theory an extension of the **Debye–Hückel theory** of dielectrics. *See also* **Kirkwood theory**.

ontogeny *or* **ontogenesis** the entire sequence of events in the development of an individual organism during its lifetime. *Compare* **phylogeny**. —**ontogenic** *or* **ontogenetic** *adj.*

oo+ *comb. form* denoting ovum or egg.

oocyte *(in zoology)* a cell of an animal ovary that undergoes meiosis to form an ovum. A **primary oocyte** is formed by differentiation of an oogonium and then undergoes the first division of meiosis to form a polar body and a secondary oocyte. Following fertilization of the egg, the **secondary oocyte** undergoes the second meiotic division to form the mature ovum and a second polar body.

oogenesis the complete process of formation and maturation of an ovum from a primordial female germ cell. —**oogenetic** *adj.*

oogonium (*pl.* **oogonia**) **1** *(in zoology)* a cell of an animal ovary that undergoes repeated mitosis, eventually forming **oocytes**. **2** *(in botany)* the female reproductive organ in certain algae and fungi. —**oogonial** *adj.*

OP *abbr. for* organophosphorus. *See* **organophosphate**.

opal codon *or* **opal triplet** *symbol*: UGA; one of the three terminator codons or **nonsense codons** in a molecule of messenger RNA.

opalescence a milky iridescence, similar to that of opal. The opalescence of some solutions is due to the reflection of light by very fine suspended particles. —**opalescent** *adj.*; **opalesce** *vb.*

opal mutant any cell or virus carrying an **opal mutation**.

opal mutation a mutation that gives rise to an **opal codon** at an abnormal position in a molecule of messenger RNA.

opal suppressor any of a number of mutations, occurring in *Escherichia coli*, that suppress an **opal codon** in messenger RNA thereby allowing insertion of one of several alternative amino acids into a polypeptide chain at that site. The mutation results in changed anticodons of the transfer RNA molecules, consequent on single-base substitution in their DNA coding sequences.

open chain *(in chemistry)* **1** a chain of atoms in a molecule that is not formed into a ring, i.e. one that has two (or more) free ends. **2 open-chain** *an alternative term for* **acyclic**.

open circle any circular duplex DNA structure containing one or more single-stranded nicks. Such a structure will dissociate at high pH into two (or more) single-stranded structures.

open circuit *(in physics)* an incomplete electrical circuit, i.e. one with infinite impedance.

open-loop system a type of system, e.g. a metabolic pathway or an electrical circuit, in which control is not exerted by feedback, each operation or activity being affected only by those earlier in the sequence. *Compare* **closed-loop system**.

open reading frame *abbr.*: ORF; a series of codon triplets, deduced from a DNA sequence, that include a 5′ **initiation codon** running through to a **termination codon**, and representing a putative or known gene. The problem often arises, e.g. in screening DNA libraries, of determining whether a stretch of DNA represents a gene. For this to be the case, it must, apart from including appropriately placed initiation and termination codons, be of a suitable length and should fulfil certain criteria indicating that the correct **reading frame** has been selected. Methods for checking this include the **RYN method**.

open system *(in thermodynamics)* any geometrically defined volume that can exchange both energy (e.g. heat or work) and matter with its surroundings. *Compare* **adiabatic system**, **closed system**.

open tetrapyrrole *see* **phycobilin**.

operand a quantity or function on which a mathematical operation is to be performed.

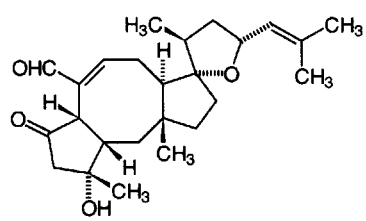
operating system *(in computing)* the software that handles input-and-output, file handling, and provides the **command language** and other user interfaces.

operator **1** *(in genetics)* a DNA sequence within an **operon** (under negative promoter control) to which a specific repressor protein can bind, thereby regulating the functioning of a **structural gene** or group of genes. **2** *(in mathematics)* a symbol (i.e. an alphabetic character, term, or special symbol) representing a particular operation to be performed on an operand or operands; e.g. Σ (= sum of), d/dx (= differentiate with respect to the variable x), + (= add to).

operon a unit of coordinated and regulated gene activity found in prokaryotes, by means of which the control of the synthesis of a protein or a group of (usually functionally associated) proteins is determined. It consists of a segment of genomic DNA containing a **structural gene** or a linear sequence of structural genes (which are transcribed as a single unit), together with one or more regulatory regions such as an **operator** (def. 1). *See also* **Jacob-Monod model**, ***lac* operon**.

ophidin *a trivial name for* 2-methylcarnosine; N^{α}-(β-alanyl)-2-methylhistidine; a constituent of snake muscle.

ophiobolin a class of sesterterpene produced only by fungi; there are six types based on the ophiobolane structure shown.



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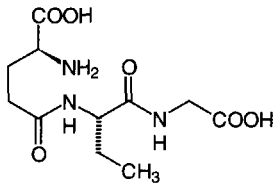
ophthalmic of, or pertaining to, the eye.

ophthalmic acid *N*-[*N*-(γ-glutamyl)-α-aminobutyryl]glycine; an analogue of glutathione in which the thiol group is replaced by a methyl group. It was originally isolated from the lens of the eye.



opiate **1** any of a group of narcotic drugs structurally related to and including **morphine** all of which are derived from opium. Apart from morphine the group includes **codeine**, **papaverine**, and **thebaine**. The term is sometimes extended to include the **opioids** (def. 1) and any other naturally occurring, semisynthetic, or synthetic narcotic substance with similar properties and whose morphine-like effects may be reversed by recognized morphine antagonists. **2** consisting of or containing **opium**; having narcotic properties similar to those of opium.

opiate receptor a membrane receptor for opiates (*see* **opioid receptor**.)

opine any of a class of unusual derivatives of basic amino acids not found in normal plant tissue but found in plant tissue that has been transformed by oncogenic plasmids from agrobacteria. The class includes the **nopaline** and **octopine** families.

opiocortin *an alternative name for* **opiomelanocortin**.

opioid **1** any nonalkaloid having **opiate**-like pharmacological effects that can be reversed by **naloxone** or other recognized morphine antagonists. **2** describing any substance having such properties.

opioid peptide any naturally occurring peptide that is an **opioid** (def. 1). Five main groups are recognized: (1) [Leu]-enkephalin and [Met]enkephalin; (2) dynorphin, α and β neoendorphin, and several other peptides that arise (or are presumed to arise) from **enkephalin** precursors; (3) α, β, γ, and δ **endorphins**, all of which are formed from β lipotropin; (4) various pronase-resistant peptides present in body fluids, e.g. β **casomorphin** (in bovine milk); (5) sundry other peptides whose opiate-like action appears to be indirect. [*Note*: In the past, the terms 'endorphin' and 'opioid peptide' were often used synonymously; it is now recommended that the former should be restricted to those opioid peptides that are derived from β lipotropin.]

opioid receptor any site on a cell surface that interacts in a highly selective manner with an opiate or an **opioid** (def. 1) and that mediates its prime pharmacological action; types μ, δ, and κ, and possibly σ have been distinguished on the basis of their response to β endorphin (End), dynorphin A (Dyn), [Met]enkephalin (Met), and [Leu]enkephalin (Leu); the potency being, for μ: End > Dyn > Met > Leu; for δ: End = Leu = Met > Dyn; and for κ: Dyn >> End >> Leu = Met. Morphine and its analogues are primarily μ agonists, but also have activity on δ and κ receptors. Effector pathways for all of these types are G-protein-mediated, μ and δ depressing cyclic AMP levels and opening a G-protein-modulated K^+ channel, κ inhibiting a G-protein-modulated Ca^{2+} channel. Some opioids also bind to other receptors known as σ, but morphine has a very low affinity for these receptors and naloxone does not block its action.

opiomelanocortin *or* **opiocortin** a polypeptide, present in the intermediate lobe of the pituitary gland, that includes within it the entire sequences of the peptide hormones **corticotropin**, α and β melanocyte stimulating hormone, β and γ **lipotropin**, and β **endorphin**. It is formed from **proopiomelanocortin**.

opium the milky, air-dried exudate from incised, unripe seed capsules of the opium poppy, *Papaver somniferum*, and some other species. Opium contains approximately 20 alkaloids, the most significant of which are **codeine**, **morphine**, **papaverine**, and **thebaine**.

OPLC *abbr. for* overpressure(d) layer chromatography.

OPRTase *see* **orotate phosphoribosyltransferase**.

opsin **1** any of a group of hydrophobic glycoproteins that occur in the visual pigments of vertebrates in equimolecular combination (as Schiff's bases) either with 11-*cis*-retinal – in **iodopsin** and **rhodopsin** – or with 3,4-didehydro-11-*cis*-retinal – in **cyanopsin** and **porphyropsin**. These opsins are of ≈35–40 kDa and consist of single-chain polypeptides glycosylated with two branched oligosaccharides. *See also* **photopsin**, **scotopsin**. **2** any of a group of proteins of ≈25 kDa that occur in combination with retinal in the purple-membrane pigments present in some strains of *Halobacterium halobium*; e.g. bacterioopsin (in bacteriorhodopsin), haloopsin (in halorhodopsin), and slow-opsin (in slow-cycling rhodopsin).

opsonify *a less common word for* **opsonize**.

opsonin any blood-serum protein that, when combined with microorganisms or other particulate material (e.g. foreign erythrocytes), increases the latter's susceptibility to phagocytosis. The two main classes are immunoglobulin G antibodies and the C3b and IC3b fragments formed from the C3 component of **complement**; other classes include **fibronectin** and the soluble mannose-binding protein of serum. An opsonin molecule acts by linking the surface of the particulate matter to a specific receptor on the surface of a phagocytic cell; commonly this receptor is either an Fc receptor (recognizing the Fc domain of an IgG immunoglobulin molecule) or a CR3 receptor (recognizing the IC3b fragment of complement). —**opsonic** *adj.*

opsonize *or* **opsonise** *or (less commonly)* **opsonify** to render (microorganisms or other particulate material) more susceptible to phagocytosis by coating with **opsonin**. —**opsonization** *or* **opsonisation** *or* **opsonification** *n.*

optic **1** *or* **optical** of or pertaining to the eye or the sense of sight; aiding vision. **2** *a less common word for* **optical** (def. 1, 2).

optical **1** *or* **optic** of, pertaining to, or involving light. **2** *or* **optic** of or pertaining to **optics**. **3** *a less common word for* **optic** (def. 1).

optical activity the ability (of chiral substances or their solutions, and chiral crystals) to rotate the plane of polarization of a transmitted beam of plane-polarized light. There is usually a correspondence between **chirality** of molecules and optical activity. *See also* **chiroptical**.

optical antipode *an older term for* **enantiomer**.

optical density *a term (no longer recommended) for* **absorbance**.

optical isomer *an older term for* **enantiomer**.

optical isomerism *an older term for* **enantiomerism**.

optically active having or displaying optical activity; the term is often used interchangeably with **chiral**.

optically inactive lacking optical activity (through being either **achiral** or **racemic**).

optical purity the ratio (usually expressed as a percentage) of the **specific optical rotation** of a sample of an enantiomeric substance to the specific optical rotation of a pure single enantiomer of the substance. *Compare* **enantiomeric purity**.

optical rotation *or* **rotation** **1** the phenomenon of rotation of the plane of polarization of plane-polarized light on its transmission by (solutions of) chiral substances, and by chiral crystals. By convention, optical rotation is designated as rightwards, or positive – and termed **dextrorotation** – when it is clockwise as seen by an observer looking towards the light source, and designated as leftwards, or negative – and termed **levorotation** – when it is anticlockwise. **2** *or* **optical rotatory power** the ability of (a solution of) a chiral substance to effect such rotation, an effect that is normally associated with **optical activity**. **3** *symbol*: α; any measure, expressed in angular degrees, of such ability under specified conditions; *see* **molar optical rotation**, **specific optical rotation**.

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optical rotatory dispersion *abbr.*: ORD; the variation of **optical rotation** with the wavelength or frequency of the transmitted light. The shape of an optical rotatory dispersion spectrum of a solution of a macromolecule often gives useful information about the conformation of the solute. *See also* **circular dichroism, Cotton effect**.

optical rotatory power *an alternative term for* **optical rotation** (def. 2).

optical system any arrangement of diffraction gratings, lenses, mirrors, prisms, etc., frequently within a specific instrument and used for a specific purpose.

optics **1** *(functioning as sing.)* the branch of physics concerned with the nature, properties, and behaviour of (visible) light and with the characteristics of optical devices, instruments, and systems. The term is extended to other kinds of electromagnetic or particulate radiation in so far as they have similar properties to light. **2** *a collective term for* an arrangement of optical components (in an instrument); the optical properties of such an arrangement.

OPTLC *abbr. for* overpressured thin-layer chromatography. *See* **overpressure(d) layer chromatography**.

oral of or pertaining to the mouth; adminstered by mouth.

orbit **1** a closed circular or near-circular course taken by a moving body (often around something). **2** the depression in the skull that contains the eye. **3** to move in or as if in an **orbit** (def. 1). *See also* **orbital**.

orbital **1** any **wave function**, Ψ, of an electron in a molecular entity. It is characterized by a particular energy value and a unique set of three quantum numbers; the counterpart in wave mechanical theory of an electron orbit in Niels Bohr's concept of atomic structure. Any particular orbital may be occupied either by one electron or by two electrons of opposed spins, or it may be unoccupied. The square of the value of Ψ at any point can be interpreted as the probability of the electron being located at that point, or as the average fractional charge density at that point. *See also* **atomic orbital, molecular orbital, pi orbital, sigma orbital**. **2** of, relating to, occupying, or moving in or as if in an **orbit** (def. 1). **3** belonging to the **orbit** (def. 2).

orbital shaker a device designed to impart an orbital motion to flasks, tubes, etc. with the purpose of mixing their contents and facilitating the transfer of gases from the gaseous to the liquid phase. It is useful especially for growing cultures of cells.

orcinol test *or* **Bial's test** a colorimetric test specific for aldopentoses. The sample is heated with strong acid to convert any aldopentose present to furfural (i.e. 2-furaldehyde), which is then reacted with orcinol (i.e. 5-methyl-1,3-benzenediol) in the presence of ferric chloride to give a blue-green compound extractable into amyl alcohol. The test is used for the determination of RNA and the detection of **pentosuria**. [After Manfred Bial (1870–1908), German physician.]

ORD *abbr. for* optical rotatory dispersion.

Ord *symbol for* a residue of the ribonucleoside orotidine (alternative to O).

order **1** *(in chemistry)* sequence (of residues in a polymer). **2 order of reaction**. **3** *(in taxonomy)* a category consisting of a number of similar families (sometimes only one family). One or more orders make up a class. **4** *(in mathematics)* the number of times a function must be differentiated to obtain a particular derivative. **5** *(in mathematics)* the number of columns or rows in a determinant or a square matrix. **6 order of magnitude**.

ordered mechanism *or* **ordered pathway** (for an enzymic reaction involving two substrates, $A + B \rightleftharpoons C$) a mechanism in which the enzyme, E, must necessarily first bind to one substrate, e.g. $E + A \rightleftharpoons EA$, and then to the second substrate, thus $EA + B \rightleftharpoons EAB$, this ternary complex then reacting to form the product, $EAB \rightleftharpoons E + C$. *Compare* **random mechanism**.

order of magnitude **1** a tenfold range of magnitude extending from a particular value either upwards or downwards. **2** a magnitude expressed to the nearest power of ten.

order of reaction *symbol*: *n*; the sum of the exponents of the concentration terms in the rate equation for an elementary chemical reaction considered in one direction only. It may also be applied to certain composite reactions.

order of reflection *symbol*: *n*; the integer, *n*, in the equation of **Bragg's law**.

ordinate the vertical, or *y*, coordinate in a plane rectangular (Cartesian) coordinate system. *Compare* **abscissa**.

ORF *abbr. for* open reading frame.

organ any part of the body of a multicellular organism that is adapted and/or specialized for the performance of one or more vital functions. The term is sometimes extended to include organelles of unicellular organisms.

organ culture a category of **tissue culture**, in which an organ, part of an organ, or an organ primordium, after removal from an animal or plant, is maintained *in vitro* in a nutrient medium with retention of its structure and/or function.

organelle any discrete structure in a unicellular organism, or in an individual cell of a multicellular organism, that is adapted and/or specialized for the performance of one or more vital functions.

organic **1** of, pertaining to, or derived from an organism or organisms. **2** of, pertaining to, or affecting an organ or organs. **3** of, relating to, or being a compound of carbon, whether or not of natural origin. **4** of any element contained in an organic compound. **5** any organic compound.

organic chemistry the branch of chemistry concerned with the compounds of carbon in covalent linkage, whether natural or artefactual, including most compounds of biological origin but excluding some simple carbon compounds, e.g. oxides, sulfides, and cyanides. *See also* **organic compound**.

organic compound any compound containing carbon in covalent linkage; various simple carbon compounds, especially carbon dioxide, carbonic acid, and salts and ions of carbonic acid, are usually excluded.

organiser *a variant spelling of* **organizer**.

organism any unicellular or multicellular prokaryote or eukaryote, usually extended to include various noncellular nucleic-acid-containing infective agents such as viruses.

organizer *or* **organiser** *(in embryology)* any part of an embryo that, through substances produced by it, stimulates the morphological development and differentiation of other parts.

organo+ *comb. form* denoting **organic** (def. 1, 2, 3).

organogenesis the formation and development of organs in an organism. —**organogenetic** *adj.*

organoleptic affecting, involving, or making use of the sense organs, especially those of smell and taste.

organomercurial **1** *or* **organomercury** of, pertaining to, or being an organic compound containing mercury, especially one in which a mercury atom is linked directly to one or more carbon atoms. **2** *or* **organomercury compound** any such compound.

organometallic **1** *or* **organometal** of, pertaining to, or being a metal-containing organic compound, especially one in which a metal atom is linked directly to one or more carbon atoms. **2** *or* **organometal compound** any such compound.

organophosphate **1** any organic compound containing a phosphoric (including fluorophosphoric, thiophosphoric, etc.) residue in amide, anhydride, ester, or thioester linkage. **2** any of a number of organophosphorus compounds originally developed as nerve gases, but formerly used as agricultural insecticides and as anthelmintics, the best known being diisopropylphosphofluoridate. These compounds inhibit serine proteases (including acetylcholinesterase, crucial for nerve transmission) by blocking an essential serine residue. *See also* **aminoethylbenzenesulfonylfluoride, diisopropyl fluorophosphonate, phenylmethylsulfonyl fluoride**.

organotroph *an alternative term for* **heterotroph(e)**.

organotrophic **1** heterotrophic; *see* **heterotroph(e)**. **2** of, pertaining to, or influencing the formation or nourishment of bodily organs.

organyl any organic substituent group, regardless of functional type, that has a single free valence at a carbon atom; e.g. ethyl, CH_3CH_2–; glycyl, $H_2NCH_2C(=O)$–; ribosyl, $C_5H_9O_4$–.

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origin *(in mathematics)* the point of intersection of a set of (usually two or three) coordinate axes; the point whose coordinates are all zero. —**original** *adj.*

O-ring a toroidal ring, usually of circular cross-section, made of neoprene or similar material and useful as a fluid- or gas-tight seal between particular parts of a device while permitting relative movement between them.

Orn *symbol for* a residue of the α-amino acid L-ornithine.

ornaline *an alternative name for* **nopalinic acid**.

ornithine *symbol*: Orn; α,δ-diaminovaleric acid; 2,5-diaminopentanoic acid; an amino acid only rarely found in proteins. L-Ornithine is an intermediate in the biosynthesis of arginine (*see* **ornithine–urea cycle**) and, in plants, of pyrrolidine and tropane alkaloids; it was first found as its dibenzoyl conjugate, **ornithuric acid**. D-ornithine is a component of **bacitracin** A.

ornithine acetyltransferase *see* **glutamate *N*-acetyltransferase**.

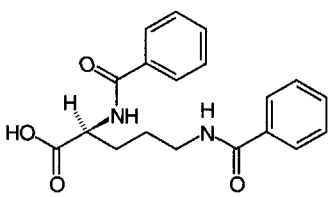
ornithine carbamoyltransferase *abbr. (in clinical chemistry)*: OCT; EC 2.1.3.3; *systematic name*: carbamoyl-phosphate:L-ornithine carbamoyltransferase; *other names*: ornithine transcarbamylase; citrulline phosphorylase. An enzyme of the **ornithine–urea cycle** that catalyses a reaction between carbamoyl phosphate and L-ornithine to form L-citrulline and orthophosphate. It is deficient in congenital **hyperammonemia**. Example, product of *argI* gene in *Escherichia coli*: database code ECARGI, 334 amino acids (36.93 kDa).

ornithine decarboxylase EC 4.1.1.17; *systematic name*: L-ornithine carboxy-lyase; an enzyme that catalyses the decarboxylation of L-ornithine to putrescine and CO_2; pyridoxal-phosphate is a coenzyme. It is the first enzyme of polyamine biosynthesis; its activity increases in the cell in response to many agonists, especially those stimulating cell growth. Example from *Neurospora crassa*: database code DCOR_NEUCR, 484 amino acids (53.24 kDa).

ornithine transacetylase *see* **glutamate *N*-acetyltransferase**.

ornithine–urea cycle *or* **ornithine cycle** *or* **arginine–urea cycle** *or* **urea cycle** a cyclic metabolic pathway, present in mammals and other ureotelic animals, that converts waste nitrogen, in the form of highly toxic ammonium, to essentially nontoxic urea, which may then be excreted. Urea is formed by hydrolysis of L-arginine to L-ornithine, the cycle being completed by conversion of ornithine to L-citrulline by carbamoylation with carbamoyl phosphate (previously formed by enzymic combination of carbon dioxide and ammonium with phosphate from ATP), reaction of the citrulline with L-aspartate to form L-argininosuccinate, and cleavage of this to produce fumarate and regenerate arginine. The cycle is also sometimes called the **Krebs cycle** or the **Krebs–Henseleit cycle**, after its discoverers. The role of argininosuccinate was revealed by the US biochemist, Sarah Ratner (1903–), in 1954.

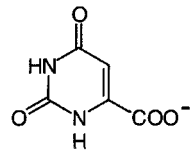
ornithuric acid *N,N′*-dibenzoylornithine; a detoxication product of benzoic acid found in the excreta of birds.



Oro *symbol for* a residue of the pyrimidine base orotate.

orosomucoid *or* **α_1-acid glycoprotein** a ≈40 kDa, water-soluble plasma protein; it consists of a single polypeptide chain with two intrachain disulfide bonds and carrying five branched, highly sialylated oligosaccharide units attached to the β-carboxyl groups of asparagine residues. Certain alleles of the gene encoding this protein have been found to be significantly increased in patients with different types of carcinoma. Example from human: database code A1AG_HUMAN, 201 amino acids (23.51 kDa).

orotate **1** *symbol*: Oro; uracil-6-carboxylate; 1,2,3,6-tetrahydro-2,6-dioxo-4-pyrimidine carboxylate; the anion of orotic acid (i.e. uracil-6-carboxylic acid). It is an intermediate in the biosynthesis of pyrimidine nucleotides from aspartate. **2** any mixture of orotic acid and its anion. **3** any salt or ester of orotic acid.



orotate phosphoribosyltransferase *abbr.*: OPRTase; EC 2.4.2.10; *other names*: orotidylic acid phosphorylase; orotidine-5′-phosphate pyrophosphorylase; an enzyme of the pathway for *de novo* biosynthesis of pyrimidines. It catalyses the formation of orotidine 5′-phosphate from orotate and 5-phospho-α-D-ribose 1-diphosphate, releasing pyrophosphate. Orotidine 5′-phosphate is decarboxylated to uridine 5′-phosphate by **orotidine-5′-phosphate decarboxylase**. Example, human protein: database code PYR5_HUMAN, 480 amino acids (52.16 kDa) – this contains domains for OPRTase (residues 1–214) and orotidine 5′-phosphate decarboxylase (residues 221–480). Deficiency causes the recessive disease **orotic aciduria** type 1.

orotic aciduria a rare hereditary disorder of pyrimidine synthesis in humans that is characterized by retarded growth, hyperchromic anemia unresponsive to the usual hematinics, and an excessive excretion of orotate in the urine. It is due to deficiency in the activities of either **orotate phosphoribosyltransferase** (EC 2.4.2.10) or **orotidine-5′-phosphate decarboxylase** (EC 4.1.1.23), or both. The condition results in the subject being a 'pyrimidine auxotroph' and can be effectively treated by administration of uracil, which both rectifies the pyrimidine deficiency and indirectly leads, through the effect of cytidine triphosphate on aspartate transcarbamoylase, to inhibition of orotate synthesis.

orotidine *symbol*: O *or* Ord; 6-carboxylatouridine; orotate riboside; 1-β-D-ribofuranosylorotate; a ribonucleoside occurring primarily as its 5′-phosphate, orotidylic acid but produced by certain mutants of *Neurospora crassa* and excreted in relatively large amounts in the urine of cancer patients treated with 6-azauridine. It is not known to be a component of ribonucleic acid.

orotidine monophosphate *abbr.*: OMP; *an alternative name for* any **orotidine phosphate**, but in particular for orotidine 5′-phosphate.

orotidine phosphate orotidine monophosphate (*abbr.*: OMP); any phosphoric monoester or diester of orotidine. Of the three possible monoesters – the 2′-phosphate, the 3′-phosphate, and the 5′-phosphate – and the two possible diesters – the 2′,3′-phosphate and the 3′,5′-phosphate – only **orotidine 5′-phosphate** is known to occur naturally (the locant therefore being omitted if no ambiguity may arise).

orotidine 5′-phosphate *or* **5′-orotidylic acid** *or* **5′-phosphoorotidine** *or* **5′-*O*-phosphonoorotidine** *symbol*: Ord5′*P*; *alternative recommended names for* orotidine monophosphate (*abbr.*: OMP), orotidine 5′-(dihydrogen phosphate), orotate ribonucleotide. (The locant is commonly omitted if there is no ambiguity as to the position of phosphorylation.) It is the immediate biosynthetic precursor of uridine monophosphate, uridylic acid, UMP, to which it is converted by decarboxylation. Thus it is important also as an intermediate in the biosynthesis of other pyrimidine nucleotides from UMP.

orotidine-5′-phosphate decarboxylase EC 4.1.1.23; *other name*: orotidylic decarboxylase; an enzyme that catalyses the

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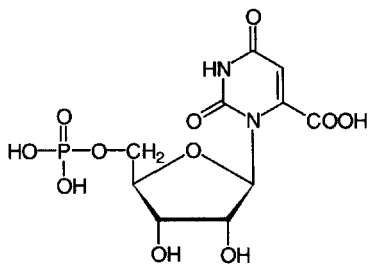
decarboxylation of orotidine 5′-phosphate to UMP a reaction carried out by the multifunctional enzyme **5′-monophosphate synthase**. Example from *Neurospora crassa*: database code DCOP_NEUCR, 397 amino acids (43.85 kDa).

orotidine-5′-phosphate pyrophosphorylase *see* **orotate phosphoribosyltransferase**.

orotidylate **1** either the monoanion or the dianion of orotidylic acid. **2** any mixture of orotidylic acid and its anions. **3** any salt or ester of orotidylic acid.

orotidylic acid *the trivial name for* any phosphoric monoester of orotidine. The position of the phosphoric residue on the ribose moiety of a given ester may be specified by a prefixed locant – *see* **orotidine phosphate**. However, 5′-orotidylic acid is the ester commonly denoted, its locant usually being omitted if no ambiguity may arise. 5′-Orotidylic acid is also an alternative recommended name for **orotidine 5′-phosphate**.



orotidylic acid phosphorylase *see* **orotate phosphoribosyltransferase**.

orotidylic decarboxylase *see* **orotidine-5′-phosphate decarboxylase**.

ortho (*followed by* to) at a position in a benzene ring adjacent to a particular (specified) substituent.

ortho- *abbr.*: *o-*; *prefix (in chemical nomenclature)* denoting an isomer of a disubstituted monocyclic aromatic compound in which the substituents are attached at positions 1 and 2 of the ring. *Compare* ***meta-***, ***para-***.

ortho+ *or (before a vowel)* **orth+** *comb. form* **1** straight or upright; perpendicular (to) or at a right angle (to); correct. **2 a** *(in inorganic chemistry)* denoting the most hydrated acid of a series of oxoacids formed from any one of certain anhydrides, or the anion or a salt formed from such an acid. The term is now approved only for orthoboric acid, H_3BO_3; orthosilicic acid, H_4SiO_4; orthophosphoric acid, H_3PO_4; orthoperiodic acid, H_5IO_6; and orthotelluric acid, H_6TeO_6. *Compare* **meta+** (def. 2), **pyro+**. **b** *(in organic chemistry)* similarly denoting hypothetical acids of general formula $RC(OH)_3$ or $C(OH)_4$ or real esters of such acids, e.g. trimethyl orthoacetate, $CH_3–C(OCH_3)_3$; tetramethyl orthocarbonate, $C(OCH_3)_4$.

***ortho-* and *peri*-fused** describing a polycyclic compound in which one ring contains two, and only two, atoms in common with each of two or more rings of a contiguous series of ***ortho*-fused** rings. Such compounds have *n* common faces and $<2n$ common atoms.

orthochromatic **1** (of a dye or stain) imparting, or capable of imparting, its own colour to a structure. **2** (of a structure) assuming, or capable of assuming, the same colour as that of a dye or stain with which it is treated. *Compare* **metachromatic**. — **orthochromatically** *adv.*

orthodox conformation the conformation adopted by a mitochondrion in the resting state when the [ATP]/[ADP] ratio is high. This is the usual conformation of mitochondria seen in electron micrographs of thin sections of intact tissue.

***ortho*-fused** describing a polycyclic compound in which any two adjacent rings contain two, and only two, atoms in common. Such compounds have *n* common faces and 2*n* common atoms.

orthogonal **1** (of axes, lines, planes, surfaces, etc.) mutually at right angles; perpendicular to one another. **2** *(in statistics)* (of a set of variates) being, or regarded as being, statistically independent.

orthograde *see* **anterograde**.

orthologous describing genes of similar function but occurring in different species.

orthomyxovirus any of a group of RNA animal viruses, in class V of the **Baltimore classification**, consisting of enveloped, pleomorphic particles 80–120 nm in diameter. The nucleocapsids are helical, 6–9 nm in diameter, and of variable length, and contain segmented RNA (minus strand); this is transcribed by a virion polymerase into complementary RNA molecules, which act as messengers. The group includes the influenza A, B, and C viruses.

orthophosphate *an alternative name for* **phosphate** (used especially to distinguish from **metaphosphate** or **pyrophosphate**). *See also* **ortho+** (def. 2a).

orthotopic transplant any tissue graft transplanted into the normal position of that tissue in the body of the recipient. *Compare* **heterotopic transplant**.

Os *symbol for* osmium.

osamine *an alternative name for* **aminodeoxysugar**.

osazone any 1,2-bis(arylhydrazone); i.e. any condensation product of the type RNH–N=CR–CR′=N–NHR formed between an α-dicarbonyl compound (e.g. a 2-ketoaldose) and hydrazine or a substituted hydrazine. α-Hydroxy- and α-amino-carbonyl compounds will also form osazones through oxidation of the corresponding [mono]hydrazones initially formed. *See also* **phenylosazone**.

oscillator an instrument or device for producing oscillations, especially an electronic device that produces an alternating output of known frequency.

oscillin a 33 kDa protein identified in sperm that induces oscillations in intracellular Ca^{2+} concentrations in mammalian eggs. It is considered to be involved in Ca^{2+} oscillations which serve as the essential trigger for egg activation and early development of the embryo.

oscillograph an instrument for producing a graphical record of an oscillating value.

oscilloscope an instrument for producing a temporary visual record of an oscillating value. A **cathode-ray oscilloscope**, based on the **cathode-ray tube**, provides a visual image of electrical signals, in the form of a graph of the signal over time.

OSCP *abbr. for* oligomycin sensitivity-conferring protein.

+ose *noun suffix* **1** originally indicating related to glucose, as either an isomer (e.g. galactose) or a polymer (e.g. cellulose, maltose), now also extended to other sugars (e.g. arabinose, fructose, sucrose) or classes of sugars (e.g. aldose, furanose, ketose, hexose, pentose, pyranose). **2** indicating the primary products of hydrolysis of a biopolymer; e.g. proteose, peptose.

Ose *(in glycolipid nomenclature) symbol for* a monosaccharide residue. A numerical subscript denotes the number of connected monosaccharide units in the oligosaccharide component, and a prefix of two or three characters represents the trivial name of the oligosaccharide; e.g. $GbOse_3$ (i.e. globatriaose), $nLcOse_4$ (i.e. neolactotetraose), $McOse_3Cer$ (i.e. mucotriosylceramide).

oside *an alternative term for* **glycoside**.

+oside *noun suffix* denoting **glycoside**.

+osis *noun suffix* denoting **1** a process or state (e.g. metamorphosis, narcosis, necrosis, osmosis). **2** a diseased condition (e.g. nephrosis, tuberculosis). **3** an increase or excess (of something) (e.g. glycogenosis, leukocytosis). *See also* **+otic**.

oskar one of the **maternal effect genes** in *Drosophila melanogaster*. It organizes the germplasm and directs localization of the germ-cell determinants. Oskar protein is required to keep *oskar* RNA and *staufen* (another maternal effect gene) protein at the posterior pole. Three other genes (*capu*, *spir*, and *stau*) are required for the initial localization of the *oskar* product to the posterior pole of the oocyte. Database code of expressed protein OSKA_DROME, 606 amino acids (69.21 kDa).

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osM *or* **osM** *symbol for* osmolar (osmol L^{-1} now recommended).
OSM *abbr. for* oncostatin M.
osmiophilic (of a structure or substance) having an affinity for, or staining readily with, osmium tetroxide; e.g. osmiophilic globules (plastoglobuli) in plastids.
osmium tetroxide osmium(VIII) oxide; OsO_4; a volatile, evil-smelling, moderately water-soluble, electron-dense substance used for fixing specimens for microscopy, especially electron microscopy, and used chemically in the hydroxylation of alkenes. The vapour is highly poisonous.
osmo+ *comb. form* denoting **1 osmosis**. **2** smell, odour.
osmoceptor *see* **osmoreceptor**.
osmol *symbol for* osmole.
osmolal **1** describing a solution that contains one **osmole** (of a specified solute), or an indicated number of osmoles, per kilogram of solvent; used also of a specified solute in such a solution. **2** describing an amount-of-substance concentration expressed in osmoles (of a specified solute) per kilogram of solvent. *Compare* **osmolar**. *See also* **osmolality**.
osmolality the concentration of osmotically active particles in an aqueous solution expressed in **osmoles** per kilogram of solvent. For a nondissociating substance the osmolality is equal to the **molality**, whereas for a substance that dissociates in aqueous solution the osmolality is greater than the molality to an extent dependent on the number of particles into which the substance dissociates and on the position of the equilibrium.
osmolar **1** describing a solution that contains one **osmole** (of a specified solute), or an indicated number of osmoles, per litre of solution; used also of a specified solute in such a solution. **2** *abbr.*: osM or osM; describing an amount-of-substance concentration expressed in osmoles (of a specified solute) per litre of solution. *Compare* **osmolal**. *See also* **osmolarity**.
osmolarity the concentration of osmotically active particles in an aqueous solution expressed in **osmoles** per litre of solution. For a nondissociating substance the osmolarity is equal to the molarity, whereas for a substance that dissociates in aqueous solution the osmolarity is greater than the molarity to an extent dependent both on the number of particles into which the substance dissociates and on the position of the equilibrium. *Compare* **osmolality**.
osmole *symbol*: osmol; the amount of substance that contains, or gives rise to, one mole of osmotically active particles when in aqueous solution.
osmometer **1** *or* **membrane osmometer** any device for demonstrating the phenomena of osmosis and osmotic pressure; any instrument for measuring osmotic pressure. **2** an apparatus for measuring the acuteness of the sense of smell. —**osmometric** *adj.*; **osmometry** *n.*
osmophile any organism that grows preferentially (or only) in media of relatively high osmotic pressure, such as ones with a high salt or sugar content. —**osmophilic** *adj.*
osmoreceptor *or* **osmoceptor** a sensory cell, or group of such cells, that is specialized to react to changes in environmental osmotic pressure, e.g. of blood plasma or of a tissue fluid. Osmoreceptors are located in the hypothalamus, in the main arteries, and at other sites.
osmoregulation the sum of the processes by which organisms regulate their internal contents of water and solutes. —**osmoregulatory** *adj.*
osmosis the spontaneous net flow of solvent by diffusion through a semipermeable membrane from a phase where the solvent has a higher chemical potential to one where the solvent has a lower chemical potential. The flow continues until the chemical potential of the solvent becomes the same on both sides of the membrane or until it is countered by a difference in hydrostatic pressure either generated or applied. —**osmotic** *adj.*; **osmotically** *adv.*; **osmose** *vb.*
osmotic coefficient *symbol*: ϕ_m (on a molality basis) *or* ϕ_x (on a mole fraction basis); the ratio of the actual to the ideal osmotic pressure of a given solution at a specified temperature; i.e. a representation of the departure of the solution from ideality.
osmotic pressure *symbol*: Π; the excess hydrostatic pressure that must be applied to a solution in order to reduce to zero the net flow of pure solvent into it by osmosis. The osmotic pressure of a dilute solution is equal to the pressure the solute would exert if it could exist as a gas at the same temperature, T, and the same amount-of-substance concentration, c; thus it may be expressed by a relation analogous to the gas equation, i.e. $\Pi = \nu cRT$ where ν is the (average) number of particles into which one solute molecule is dissociated under the given conditions, and R is the gas constant. Osmotic pressure is a **colligative property** of a solution. *See also* **colloid osmotic pressure**, **oncotic pressure**.
osmotic shock any disruption or other disturbance caused to suspended cells or cell organelles by a sudden change in the osmotic pressure of their suspending medium.
osmotolerant describing a cell or organism that is tolerant to a wide range of osmotic pressures in its environment.
osone any 2-ketoaldose; use not recommended.
ossein the organic material, consisting mainly of collagen, that remains after treatment of bone with dilute acid to dissolve out the inorganic components.
ossify to make into bone or to become bone. —**ossification** *n.*
osteo+ *or (before a vowel)* **oste+** *or (sometimes)* **ost+** *comb. form* denoting bone.
osteoblast a mesenchymal cell that secretes the organic matrix of bone (i.e. osteoid, consisting chiefly of collagen); as the matrix becomes calcified the osteoblast becomes trapped and is known as an osteocyte.
osteocalcin *other names*: γ-carboxyglutamic acid-containing protein; bone GLA-protein (*abbr.*: BGP); a protein that binds Ca^{2+} and apatite; the binding depends on γ-carboxyglutamic acid residues (three per molecule) formed by vitamin K-dependent carboxylation. Example (precursor) from human: database code OSTC_HUMAN, 100 amino acids (10.95 kDa).
osteoclast a large, multinucleate **macrophage** that erodes bone matrix and is able to tunnel deep into the substance of compact bone. Osteoclasts are formed by the fusion of blood monocytes and play an important role in the remodelling of bone and the removal of dead bone.
osteocyte an osteoblast when it has become trapped in a lacuna of the bone matrix and is no longer able to divide or secrete appreciable amounts of new matrix. Osteocytes are connected by fine cellular processes that pass through the bone canaliculi.
osteogenesis the processes of bone formation; ossification.
osteogenesis imperfecta a genetically heterogeneous group of human diseases in which there is disorder of connective tissue affecting not only bone but also tendons, ligaments, fascia, etc. The bones are unusually brittle and liable to fracture and in **osteogenesis imperfecta congenita** in the neonate there is evidence that the collagen of bone matrix may be abnormal.
osteoid **1** the unmineralized bone matrix secreted by osteoblasts; it consists chiefly of collagen. **2** resembling bone.
osteolysis the breakdown and dissolution of bone, especially through disease. —**osteolytic** *adj.*
osteomalacia a clinical condition of adults characterized by softening and deformation of the bones due to a failure to maintain their mineralization. It has a wide variety of possible causes, of which dietary deficiencies of vitamin D, calcium, or phosphate are the commonest.
osteonectin *see* **SPARC**.
osteopontin *other names*: bone sialoprotein 1; urinary stone protein; secreted phosphoprotein 1 (*abbr.*: SPP-1); nephropontin; uropontin; a bone-specific sialoprotein produced by cells in osteoid matrix but independently discovered from several different functions. It can form a bridge between cells and the mineral in the matrix, and is found at high concentrations on the cement lines where bone formation follows resorption. It is also found in the kidney, and plays a principal role in urinary

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stone formation. In arterial smooth muscle cells, its level increases in atherosclerotic plaques. It is secreted, binds calcium, and binds covalently to fibronectin. It has an **RGD** integrin-binding sequence and is one of the major ligands for the vitronectin receptor. It is phosphorylated on serine, and is an *O*- and *N*-glycosylated protein. There are two forms from alternative splicing. Example (precursor) from human: database code OSTP_HUMAN, 314 amino acids (35.38 kDa).

osteoporosis a clinical condition characterized by a general or local reduction in bone mass with little alteration in gross composition. This causes the affected bones to become porous, brittle, and liable to fracture. Generalized osteoporosis is often hormonal in origin.

Ostwald, Friedrich Wilhelm (1853–1932), Russian-born German chemist; noted also for his work on electrochemistry and for the invention of an industrially important process for the catalytic oxidation of ammonia to nitric acid; Nobel Laureate in Chemistry (1909) 'in recognition of his work on catalysis and for his investigations into the fundamental principles governing chemical equilibria and rates of reaction'.

Ostwald dilution law a relationship, deduced by **Ostwald** (1888), between the amount-of-substance concentration, c, and the degree of dissociation, α, of a weak electrolyte. It is given by:

$$\alpha^2 c/(1 - \alpha) = K,$$

where K is the apparent dissociation constant of the electrolyte.

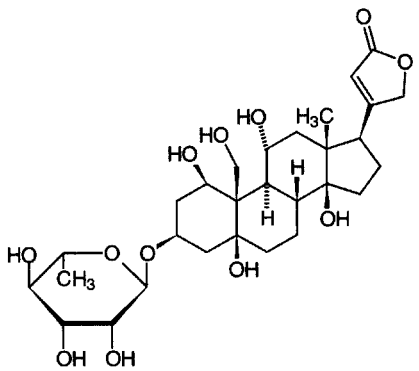
Ostwald pipette a pipette for measuring small volumes of liquids, especially viscous liquids. It features a capillary stem and delivery jet and a shoulderless bulb near the jet. Various modifications have been described.

Ostwald viscometer a simple **capillary viscometer**.

+osyl *suffix* indicating a **glycosyl** group.

+otic *suffix forming adjectives and nouns* **1** affected by (e.g. necrotic) or relating to (e.g. osmotic). **2** causing (e.g. mitotic, narcotic). —**+otically** *adv.*

ouabain *or* **G-strophanthin** a **cardiac glycoside** whose carbohydrate moiety is L-rhamnose, obtained from the seeds of *Strophanthus gratus*. It is a specific inhibitor of the membrane-bound sodium pump Na^+,K^+-ATPase (*see* **sodium/potassium ATPase**) of animal cells.



Ouchterlony technique a development of **double immunodiffusion**, effected in two dimensions so that comparisons can be made between two or more antigen-containing samples in their reaction with one antiserum. The particular pattern of precipitation lines or arcs formed enables conclusions to be drawn regarding the identity, partial identity, or nonidentity of antigens in the various samples examined. [After O. Ouchterlony, French immunologist.]

Oudin technique a simple, single immunodiffusion technique, effected in one dimension, in which a solution of an antigen-containing sample is placed above a column of antiserum incorporated in a gel in a tube; antigen diffuses into the gel, where it reacts with antibody to form one or more precipitation bands. [After Jacques Oudin (1923–).]

ounce *symbol*: oz; a unit of mass, equal in the avoirdupois system to one-sixteenth of a pound (= 28.3495 grams). This must be distinguished from the **troy ounce** (equal to 480 grains, 31.1035 grams).

outer membrane **1** *(in eukaryotes)* the more external of the two membranes that surround a chloroplast, a mitochondrion, or a nucleus. **2** *(in prokaryotes)* the layer of lipopolysaccharide, lipoprotein, and protein that lies external to the peptidoglycan in the cell wall of a Gram-negative bacterium.

outer membrane protein P68 *see* **pertactin**.

outlier *(in statistics)* any member of a set of observations that is so far removed in value from the remaining members that its validity is questionable.

ov+ *a variant form of* **ovi+** (before a vowel).

ova the plural of **ovum**.

ovalbumin *abbr.*: OA; a ≈44.5 kDa glycoprotein, also called egg albumin, that is the major protein of egg white from hens' eggs. Each molecule consists of a single polypeptide chain and carries a single oligosaccharide chain containing only mannose and *N*-acetylglucosamine residues; one or two phospho groups also may be present. It is included in the **serpin** family. It is synthesized by the oviduct under hormonal control. Although it is a secreted protein, it has no N-terminal signal peptide. Example from chicken: database code OVAL_CHICK, 385 amino acids (42.70 kDa); 3-D structure known.

ovarian hormone any of the numerous steroid hormones secreted by the ovary.

ovary **1** *(in zoology)* the gonad of a female animal; vertebrates have a pair of ovaries. The ovary contains oocytes from which ova are produced, and it also secretes various steroid hormones. Its activity is cyclical and is controlled by gonadotropin(s). **2** *(in botany)* the enlarged basal part of a carpel or a syncarpous gynecium of a flower that contains one or more ovules. —**ovarian** *adj.*

overgrowth **1** excessive growth; hyperplasia. **2** a later but more vigorous growth by another strain or species of organism that supplants one already existing.

Overhauser effect *or* **Overhauser enhancement** *see* **nuclear Overhauser effect**.

overlap peptide a fragment, produced by partial hydrolysis of a polypeptide or protein, that contains both the N-terminal part of the sequence of one further peptide fragment and the C-terminal part of the sequence of a second further peptide fragment, and enables those two to be placed in the correct position in the overall sequence of the parent compound during protein sequencing procedures.

overlapping code a code in which one element of a code-word forms part of an adjacent code-word in an encoded piece of information. A triplet code (such as the **genetic code**, where the code-words are codons) may be either: a **fully overlapping code**, in which one code-word consists of the elements at positions n, $(n+1)$, $(n+2)$, and the next code-word consists of the elements at positions $(n+1)$, $(n+2)$, $(n+3)$; or a **partially overlapping code**, in which adjacent code-words comprise elements at n, $(n+1)$, $(n+2)$, and those at $(n+2)$, $(n+3)$, $(n+4)$. In a **nonoverlapping code**, such as the genetic code proved to be, no element of one code-word forms part of an adjacent code-word.

overlapping gene any gene whose polynucleotide sequence overlaps, wholly or in part, that of another gene in the same stretch of a genome. The codons may or may not be in the same **reading frame**. In mitochondria and some viruses, some mRNAs are synthesized by the transcription of the same DNA using different reading frames.

overpressure(d) layer chromatography *abbr.*: OPLC; a chromatographic technique that gives some of the advantages of **high-pressure liquid chromatography** to **thin-layer chromatography**, with resultant increases in both speed and efficiency of separa-

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tion. The sorbent layer is completely covered by a flexible membrane under external pressure and the solvent is pumped continuously through the sorbent layer.

overshoot the extent to which a control system causes the variable being controlled to go initially beyond its final equilibrium position.

ovi+ *or* **ovo+** *or (before a vowel)* **ov+** *comb. form* denoting ovum or egg.

oviduct *(in zoology)* the tube through which ova are conveyed from the ovary to the exterior or to some intermediate organ such as the uterus. In mammals it is known more commonly as the **Fallopian tube** or **uterine tube**.

oviductin *other name*: gp43 processing protease; a high molecular weight glycoprotein that is secreted by the nonciliated secretory cells of the oviduct and later transferred to the zona pellucida of the oocyte during oviductal transit. It processes a 43 kDa glycoprotein of the oocyte envelope during its transit through the duct. Example from golden hamster: database code MAU15048, 635 amino acids (69.36 kDa).

ovine *abbr.*: o *or (formerly)* O; of, belonging to, characteristic of, obtained from, or being sheep or a sheep; resembling a sheep, sheeplike.

ovo+ *a variant form of* **ovi+**.

ovoflavin *or* **oviflavine** *a former name for* **riboflavin**.

ovoinhibitor a contaminant of crude **ovomucoid** that, unlike pure ovomucoid, inhibits chymotrypsin as well as trypsin.

ovomucoid a glycoprotein found in egg white from hens' eggs; it is an inhibitor of trypsin. Example from *Gallus gallus*: database code IOVO_CHICK, 210 amino acids (22.59 kDa).

ovothiol a novel thiohistidine compound from sea-urchin eggs that confers NAD(P)H-O_2 oxidoreductase activity on ovoperoxidase.

ovotransferrin *an alternative name for* **conalbumin**.

ovulate to discharge an egg or eggs from an ovary. —**ovulation** *n.*

ovule **1** *(in botany)* a structure in the ovary of a seed plant that develops into a seed after fertilization of the egg cell within it. **2** *(in zoology)* a small, especially immature, ovum or egg.

ovum (*pl.* **ova**) *(in zoology)* strictly, an unfertilized egg cell, i.e. female gamete, which contains a haploid nucleus and which on fertilization has the unique ability to develop into a new individual. In many animals, mammals included, **oogenesis** is arrested and meiosis is not completed until after fertilization of the secondary **oocyte**, hence in these animals an ovum in the strict sense cannot exist. However, the term is often applied instead either to the secondary oocyte or to the product resulting from the second meiotic division after fertilization.

OWL a composite protein database (University of Leeds, UK). *See* **Appendix E**.

oxa+ *or (sometimes before a vowel)* **ox+** *prefix (in chemical nomenclature)* denoting replacement of a methylene group in a specified acyclic or monocyclic hydrocarbon by an oxygen atom. For certain natural products, (e.g. tetrapyrroles), the meaning is extended to denote replacement of a noncarbon atom (with any attached hydrogen atoms) by an oxygen atom.

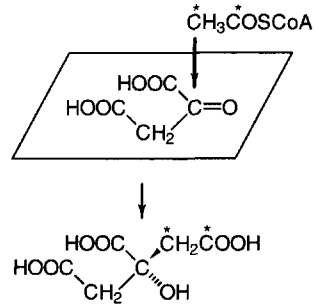
oxalacetate *an alternative name for* **oxaloacetate**.

oxalate **1** *the trivial name for* ethanedioate, $^{-}OOC–COO^{-}$, the dianion of oxalic acid, i.e. ethanedioic acid. It occurs in many plants, especially sorrels of the genera *Oxalis* and *Rumex*, and is highly toxic to animals. Normally, small amounts are formed in humans and excreted in the urine; larger amounts occur in patients with **hyperoxaluria**. The calcium salt is virtually insoluble in water, a property that is valuable in the determination of calcium and in the use of oxalate *in vitro* as an anticoagulant. **2** any mixture of free oxalic acid and its mono-ions and dianions. **3** any salt or ester of oxalic acid.

oxalo the univalent acyl group, HOOC–CO–, derived from oxalic acid by loss of one hydroxyl group. *See also* **oxalyl** (def. 1).

oxalo+ *prefix* indicating the presence of an **oxalo** group.

oxaloacetate *or* **oxalacetate** *abbr.*: OAA; **1** *the trivial name for* oxosuccinate (*formerly* ketosuccinate); oxobutanedioate; $^{-}OOC–CO–CH_2–COO^{-}$ (keto form) or $^{-}OOC–C(OH)=CH–COO^{-}$ (enol form); the dianion of oxaloacetic acid. It is an important intermediate in metabolism, especially as a component of the **tricarboxylic-acid cycle**. The stereochemistry of the **citrate (*Si*)-synthase** reaction is shown below.



2 any mixture of free oxaloacetic acid and its mono- and dianions. **3** any salt or ester of oxaloacetic acid.

oxalosis the renal and extrarenal deposition of calcium oxalate (*see* **oxalate**) seen in patients with **hyperoxaluria**.

oxalosuccinate **1** *the trivial name for* 2-oxotricarballylate *(formerly* α-ketotricarballylate); 1-oxopropane-1,2,3-tricarboxylate; $^{-}OOC–CO–CH(COO^{-})–CH_2–COO^{-}$; the trianion of oxalosuccinic acid. It is an enzyme-bound intermediate in the conversion of isocitrate to 2-oxoglutarate by **isocitrate dehydrogenase (NAD$^+$)** in the **tricarboxylic-acid cycle**. **2** any mixture of free oxalosuccinic acid and its mono- and dianions. **3** any salt or ester of oxalosuccinic acid.

oxaluria *an alternative name for* **hyperoxaluria**.

oxalyl **1** *(in biochemistry) (sometimes) an alternative name for* **oxalo**. **2** *(in chemistry)* the divalent diacyl group, –CO–CO–, derived from oxalic acid by loss of both hydroxyl groups.

OXBOX a 13 bp sequence (present in the region –123 to –674 bp) of the heart and skeletal muscle gene for the adenine nucleotide translocator and also in the promoter region of the gene for human ATP synthase β subunit. It appears to be a positive translational element.

oxene a reactive species of oxygen involved in the hydroxylation reaction catalysed by cytochrome P450; it is iron-bound oxygen which is electron deficient but electrically neutral –P450–Fe^{3+}–O. It reacts with the bound substrate to release the hydroxylated substrate with the regeneration of P450–Fe^{3+}.

oxidant the chemical species that accepts one or more electrons in a redox reaction; i.e. the species that undergoes reduction in such a reaction. *Compare* **reductant**.

oxidase any **oxidoreductase** that catalyses a reaction in which dioxygen is the electron acceptor (i.e. **oxidant**).

oxidase test a test for the presence of cytochrome *c* oxidase in bacteria that depends on the oxidation of tetramethyl-*p*-phenylenediamine to a violet-coloured product. It is useful for primary characterization, especially of Gram-negative organisms.

oxidation **1** the action or process of reacting with oxygen, especially the addition of oxygen to a substance. **2** the loss or removal of hydrogen from a substance. **3** the loss or removal of one or more electrons from a molecular entity, with or without concomitant loss or removal of a proton or protons. In this sense, oxidation is the opposite of, and is always coupled to, **reduction**. **4** the increase to a more positive value of the **oxidation number** of an atom, whether the atom is uncharged or charged, and whether free or covalently bound. —**oxidative** *adj.*

***α*-oxidation** *see* **alpha-oxidation**.

***β*-oxidation** *see* **beta-oxidation**.

***ω*-oxidation** *see* **omega-oxidation**.

oxidation level *or* **oxidation state** the status of an organic compound in terms of whether it can be considered to undergo ox-

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idation or reduction (or neither) upon conversion to a related compound. If conversion involves oxidation, the parent compound is said to have a higher oxidation level than the product; if conversion involves reduction, the parent compound is said to have a lower oxidation level. The term is thus used in a relative rather than an absolute sense. *See also* **oxidation number**.

oxidation number *or* **oxidation state** a number assigned to a particular atom in a molecular entity that represents, actually or notionally, the charge on that atom. Thus, atoms of pure elements have an oxidation number of zero; in molecules of simple electrovalent compounds the oxidation number of each component atom is equal to the charge on the respective ion; and in molecules of covalent compounds the notional charge on a particular atom is derived by assigning electrons to the more electronegative partner in each bond involving the atom in question. By convention, hydrogen is considered to have an oxidation number of +1 when in combination with nonmetals. The oxidation number of a carbon atom can range from –4 (e.g. in CH_4) through zero (e.g. in CH_2O or solid C) to +4 (e.g. in CO_2). The oxidation number of an atom may be indicated by a Roman numeral; e.g. iron(III) oxide, ferric oxide, Fe_2O_3. The algebraic sum of the oxidation numbers of all the atoms in any molecular entity must equal the charge on that entity.

oxidation potential a measure of the tendency of a substance to oxidize spontaneously through loss of electrons. It is the standard potential of the half-reaction: $A \rightarrow A^{n+} + ne$ and is equal to the **reduction potential** but of opposite sign.

oxidation–reduction *an alternative term for* **redox**.

oxidation–reduction indicator *an alternative term for* **redox indicator**.

oxidation–reduction potential *an alternative term for* **redox potential**.

oxidation state **1** *an alternative term for* **oxidation number**. **2** *an alternative term for* **oxidation level** (less preferred).

oxidative deamination deamination with concomitant oxidation, as in the enzymic conversion, regardless of the nature of the electron acceptor, of an α-amino acid to an α-oxo acid. *Compare* **reductive amination**.

oxidative decarboxylation decarboxylation with concomitant oxidation, as in the enzymic conversion, regardless of the nature of the electron acceptor, of an α-oxo acid (actually or formally) to a carboxylic acid containing one less carbon atom.

oxidative metabolism *an alternative term for* **respiration** (def. 1).

oxidative pentose phosphate pathway *or* **hexose monophosphate shunt** an alternative route additional to glycolysis in plants that generates: (1) NADPH when it is not being formed by photosynthesis; (2) ribose 5-phosphate required in the biosynthesis of nucleosides; and (3) erythrose 4-phosphate required for biosynthesis of shikimic acid, a key intermediate in the formation of aromatic rings. *See also* **pentose phosphate pathway**.

oxidative phosphorylation *or* **respiratory-chain phosphorylation** the phosphorylation of ADP to ATP that accompanies the oxidation of a metabolite through the operation of the **respiratory chain**. The overall reaction may be summarized by the equation:

$$AH_2 + 0.5O_2 + xP_i + xADP \rightarrow A + (x+1)H_2O + xATP$$

where AH_2 is an oxidizable metabolite, A is the product of the oxidation, P_i is inorganic orthophosphate, and x has a value between 1 and 3 depending on the nature of AH_2 and the functional state of the respiratory chain. The proton gradient built up across the inner mitochondrial membrane by the proton pumps of the respiratory chain drives ATP synthesis by the **H^+-transporting ATP synthase**. *See also* **chemiosmotic coupling hypothesis**.

oxide **1** *(in inorganic chemistry)* any binary compound of oxygen and some other element. **2** *an alternative generic name for* any cyclic ether that is an **oxirane**; such a compound is named as the oxide of the alkene from which it may be formed through addition of an atom of oxygen across the double bond; e.g. ethylene oxide, C_2H_4O. **3** *a term used in some languages for* **ether**. **4** any compound in which an oxygen atom has been attached to a heteroatom of a precursor compound. This definition includes compounds of general formulae: RC≡NO (nitrile oxides; e.g. benzonitrile oxide), >C=N(O)R or R,R′,R″NO (*N*-oxides, amine oxides; e.g. trimethylamine oxide); and R,R′SO (*S*-oxides, sulfoxides; e.g. methionine *S*-oxide; dimethyl sulfoxide).

+oxide *or* **+olate** *suffix* denoting **1** an anion formed by loss of a proton from the hydroxyl group of an alcohol or phenol; e.g. ethoxide ion, $C_2H_5O^-$. **2** a compound of such an anion with a cation; e.g. sodium phenoxide (i.e. sodium phenolate), C_6H_5ONa. *See also* **epoxide**, **hydroperoxide**, **hydroxide**, **nitroxide**, **peroxide**, **sulfoxide**, **superoxide**.

oxidize *or* **oxidise** **1** to undergo or effect **oxidation**. **2** to form or cause to form a superficial layer of oxide on a metal. *Compare* **reduce**. —**oxidization** *or* **oxidisation** *n.*

oxidizer *or* **oxidiser** **1** *a less common name for* **oxidizing agent**. **2** a device for effecting a particular oxidation.

oxidizing agent *or* **oxidising agent** any substance or mixture used for effecting **oxidation**.

oxidoreductase *the systematic name for* any enzyme of class EC 1. These enzymes catalyse oxidation–reduction (i.e. **redox**) reactions and the class comprises **dehydrogenases**, **oxidases**, and **reductases**.

oxidoreduction *an alternative term for* **redox**.

oximeter any photometric device for (continuously) measuring the oxyhemoglobin/hemoglobin ratio in blood, either *in vivo* or *in vitro*.

oxine *the trivial name for* 8-hydroxyquinoline; 8-quinolinol. With many species of metal ion this compound forms water-insoluble chelate complexes and thereby is useful in analysis. It is also a disinfectant, and, as the copper chelate, is an effective fungicide.

oxirane **1** *the class name for* any compound containing a three-membered saturated ring comprising two carbon atoms and one oxygen atom. **2** *the systematic name for* the type member of this class, known commonly as ethylene oxide, C_2H_4O.

oxo **1** the chemical group consisting of an oxygen atom, =O, doubly bonded to another atom (often of carbon) in a molecular structure. When bonded to a carbon atom it forms the carbonyl group, >C=O. *Compare* **oxy**. **2** *or (formerly)* **oxo+** modifying the class-name of a chemical compound to indicate the presence of an oxo group as a substituent in place of two hydrogen atoms; e.g. **oxocarboxylic acid**. The position of substitution may be specified by a predfixed locant; e.g. 17-oxosteroid. *See also* **keto** (def. 3). *Compare* **oxo** (def. 1).

oxo+ *or (sometimes before a vowel)* **ox+** **1** *prefix (in chemical nomenclature)* indicating substitution of a doubly bonded oxygen atom into a specified compound or group by the (formal or actual) oxidation of a methylene group, $>CH_2$, to a keto group, >C=O, or of a methyl group, $-CH_3$, to a formyl group, –CH=O, with the production of a ketone or an aldehyde respectively; e.g. oxoglutaric acid (*see* **oxoglutarate**), 3,6-dioxohexanoic acid (*or* 5-formyl-3-oxopentanoic acid). *Compare* **oxo** (def. 2). **2** *comb. form* denoting presence of one or more (singly or doubly bonded) oxygen atoms in a molecular structure; e.g. **oxoacid**, **oxonium**.

oxoacid **1** *the recommended term for* any compound whose molecular structure contains oxygen, at least one other element, and at least one atom of hydrogen bound to oxygen, and also that yields a conjugate base (*see* **oxoanion**) by loss of a hydron. Examples include: hypochlorous acid, ClOH; sulfurous acid, $O=S(OH)_2$; nitric acid, (O=)NOH; [ortho]phosphoric acid, $O=P(OH)_3$; and also any phosphonic acid, $RP(=O)(OH)_2$, and any carboxylic acid, RC(=O)OH (where R = H or hydrocarbyl). *See also* oxocarboxylic acid. **2** *or* **oxo acid** *or* **oxyacid** *or* **oxy-acid** *the traditional name, now obsolete, for* any acid having oxygen in its acidic function, as opposed

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to a 'hydracid' where oxygen is lacking (e.g. hydrochloric acid, HCl).

oxo acid **1** *see* **oxocarboxylic acid**. **2** *a variant of* **oxoacid** (def. 2).

3-oxoacid CoA-transferase EC 2.8.3.5; *other name*: succinyl-CoA:3-ketoacid-CoA transferase; an enzyme that catalyses the reaction:

succinyl-CoA + 3-oxo acid = succinate + 3-oxoacyl-CoA.

In mammals it converts plasma acetoacetate that has been taken up by tissues into acetoacetyl-CoA for further metabolism. Example from pig: database code A41771, 520 amino acids (56.34 kDa).

3-oxoacyl-[acyl-carrier protein] reductase (NADH) EC 1.1.1.212; an enzyme that catalyses the reduction by NADH of 3-oxoacyl-[acyl-carrier protein] to (3*R*)-3-hydroxyacyl-[acyl-carrier protein] with formation of NAD^+. This is one of the steps of fatty-acid synthesis in plants. *Compare* **fatty acid synthase complex**.

oxoanion *or (formerly)* **oxo anion** *or* **oxyanion** *or* **oxy-anion** any of the possible anions formable from a molecule of an **oxoacid** (def. 1) by loss of one or more hydrons.

oxobutanedioate *see* **oxaloacetate**.

oxocarboxylic acid *the recommended name for* any **carboxylic acid** that contains an aldehydic group attached to, or/and one or more ketonic groups contained in, its principal chain or parent ring system, i.e. any into which one or more oxo groups have been substituted. The term is commonly shortened to **oxo acid**, but the full name should be used wherever confusion with **oxoacid** is possible. The older term keto acid is often still used (*see* **keto** (def. 3)).

17-oxogenic steroid *or (formerly)* **17-ketogenic steroid** any urinary corticosteroid or its metabolites that can be estimated by the **Zimmermann reaction** after oxidation to the corresponding 17-oxo steroid.

oxoglutarate *or (formerly)* **ketoglutarate**; **1** 2-oxoglutarate *or* α-oxoglutarate 2-oxopentanedioate; $^-OOC–[CH_2]_2–CO–COO^-$; the dianion of 2-oxoglutaric acid (i.e. 2-oxopentanedioic acid), an α-oxo (carboxylic) acid. It is a key constituent of the tricarboxylic-acid cycle and a key intermediate in amino-acid metabolism. In the cycle it is formed by oxidative decarboxylation of isocitrate and converted into a further oxidative decarboxylation reaction to succinyl-coenzyme A. It may also be formed from or converted into glutamate (and thus several other amino acids indirectly) by transamination, or formed by degradation of lysine via glutarate and 2-hydroxyglutarate. The older name **α-ketoglutarate** is often still used. **2** 3-oxoglutarate *or* β-oxoglutarate acetonedicarboxylate; 3-oxopentanedioate; $^-OOC–CH_2–CO–CH_2–COO^-$; the dianion of 3-oxoglutaric acid (i.e. 3-oxopentanedioic acid), a β-oxo (carboxylic) acid. It is a product of the action of the mould *Aspergillus niger* on citrate.

oxoglutarate decarboxylase *see* **oxoglutarate dehydrogenase (lipoamide)**.

oxoglutarate dehydrogenase complex an enzyme complex, closely analogous in mechanism to the **pyruvate dehydrogenase complex**. It accomplishes the overall reaction:

2-oxoglutarate + CoA + NAD^+ =
succinyl-CoA + CO_2 + NADH.

It consists of three activities: **oxoglutarate dehydrogenase (lipoamide)**, the E_1 component; **dihydrolipoamide *S*-succinyltransferase**, the E_2 component; and **dihydrolipoamide dehydrogenase**, the E_3 component (this being identical to the E_3 component of the pyruvate dehydrogenase complex).

oxoglutarate dehydrogenase (lipoamide) EC 1.2.4.2; *other names*: oxoglutarate decarboxylase; α-ketoglutaric dehydrogenase; an enzyme that catalyses the reaction between 2-oxoglutarate and lipoamide to form *S*-succinyldihydrolipoamide with release of CO_2. This is the E_1 component of the **oxoglutarate dehydrogenase complex**. Thiamine diphosphate is a coenzyme. Examples: 2-oxoglutarate dehydrogenase E_1 component (α-ketoglutarate dehydrogenase) from *Escherichia coli*: database code ODO1_ECOLI, 933 amino acids (104.93 kDa); E_1 component (precursor) from human: database code ODO1_HUMAN, 1003 amino acids (113.11 kDa).

oxoglutarate/malate carrier protein *see* **OGCP**.

2-oxoisovalerate dehydrogenase *see* **3-methyl-2-oxobutanoate dehydrogenase (lipoamide)**.

oxolinic acid 5-ethyl-5,8-dihydro-8-oxo-1,3-dioxolo[4,5-g]quinoline-7-carboxylic acid; a **4-quinolone antibiotic** with antibacterial activity through inhibition of bacterial DNA gyrase.

oxonium **1** *or (formerly)* **hydronium** *or* **hydroxonium** the ion, H_3O^+, formed by covalent linkage of a hydron to a single water molecule. *Compare* **H^+(aq)**. **2** any organic entity in which an oxygen atom is linked to three groups (one or two of which may be –H) and bears a formal single positive charge.

(5-)oxoproline *symbol*: Glp *or* <Glu; *the recommended trivial name for* pyroglutamic acid; pyrrolidone carboxylic acid; 5-oxopyrrolidine-2-carboxylic acid; a **noncoded amino acid**. It occurs at the N terminus of certain peptide hormones and is an intermediate in the γ-glutamyl cycle. *Compare* **oxyproline**.

oxo steroid *or* **keto steroid** any steroid having an oxo substituent in its molecular structure, whether in the ring system (as part of a ketonic group) or in a side chain (as part of either a ketonic or an aldehydic group). The position of substitution may be specified by a prefixed locant. The term **17-oxo steroid** (or 17-keto steroid) usually refers specifically to any of a group of androgens and their metabolites that are present in urine and that can be extracted and estimated by the **Zimmermann reaction**. The amount of steroids excreted in the urine has been used as an index of androgen production in the body.

oxosuccinate *see* **oxaloacetate**.

oxphos *a colloquial term for* **oxidative phosphorylation**.

OXT *abbr. for* oxytocin.

oxy the chemical group consisting of an oxygen atom, –O–, singly bonded to two carbon atoms in a molecular structure, e.g. of an epoxide, an ester, or an ether. *Compare* **oxo**.

oxy+ *prefix* denoting **1** *(in organic chemical nomenclature)* the presence of an oxygen atom directly attached (by single covalent bonds) to two moieties of the same indicated parent compound, with formation of a symmetrical ether, where there is a functional group or substituent in the parent compound that has priority over 'ether' for citation as the principal characteristic group; e.g. 3,3′-oxydipropanoic acid (*not* bis(3-carboxypropyl) ether). *See also* **epoxy+**. **2** *(obsolete in organic chemical nomenclature but retained in pharmaceutical nomenclature)* substitution of a hydroxyl group for a hydrogen atom; e.g. oxyproline (*now* hydroxyproline), oxytetracycline. **3** *(in inorganic chemical nomenclature)* formation of a 'basic' (i.e. double) salt containing the oxide anion, O^{2-}, and a specified second anion; e.g. bismuth oxychloride (i.e. bismuth chloride oxide). **4** *or* **oxy-** presence of oxygen in the acidic function of an acid or in the corresponding moiety of a derived anion (obsolete; *see* **oxoacid** (def. 2), **oxoanion**). *comb. form* indicating. **5** dioxygen; e.g. oxybiotic, oxyhemoglobin, oxyhydrogen. **6** oxidation; e.g. oxycellulose. **7** acid; e.g. **oxyntic**.

oxyacid *or* **oxy-acid** *a variant of* **oxoacid** (def. 2).

oxyanion *or* **oxy-anion** *(formerly) a variant of* **oxoanion**.

oxybiontic *or* **oxybiotic** living in the presence of oxygen; aerobic.

oxycellulose any of the various materials obtained by the oxidation of cellulose. Such materials are useful as cation-exchangers or for fabrication into lint and gauzes.

oxygen **1** *symbol*: O; a nonmetallic element of group 16 of the (IUPAC) **periodic table**; atomic number 8; relative atomic mass 15.9994. Naturally occurring oxygen consists of a mixture of three stable nuclides of relative masses 16 (99.759 atom percent), 17 (0.037 atom percent), and 18 (0.204 atom percent). The latter, commonly known as **heavy oxygen**, is useful as a tracer in studies of chemical and biochemical reaction mechanisms. The commonest valence is two. Oxygen is the most

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abundant element in the biosphere: in the atmosphere it occurs elementally in the form of molecules of the diatomic gas dioxygen, which comprises 20.95% by volume of dry air, and as traces of the gas **ozone** (i.e. trioxygen). The atmosphere also contains small amounts of the oxygen compounds carbon dioxide and water (vapour); almost half by weight of the surface of the Earth consists of oxygen in combined form, principally as water and silicates. **2** *or* **molecular oxygen** *symbol*: O_2; *the common name for* the gas correctly known as **dioxygen**.

oxygen-15 the radioactive nuclide of oxygen, $^{15}_{8}O$. It is prepared in a cyclotron by bombarding $^{17}_{7}N$ with deuterons, the products being $^{15}_{8}O$ and neutrons. It emits a positron, β^+ (0.511 MeV), and has a half-life of 2 min; it is used in positron emission **tomography**.

oxygenase any oxidoreductase enzyme catalysing a reaction in which dioxygen is the electron acceptor. Such enzymes may be either **monooxygenases** or **dioxygenases** (with the exception of certain uncharacterized enzymes forming EC sub-subclass 1.13.99).

oxygenate **1** to mix, supply, or treat with dioxygen; to saturate a fluid, especially blood, culture medium, etc., with dioxygen. **2** to cause the combination of an oxygen-carrying or oxygen-storing protein with dioxygen; to undergo such a reaction. —**oxygenation** *n.*

oxygenator an apparatus for oxygenation, especially of blood.

oxygen cycle the sum total of the processes via which atmospheric dioxygen is exchanged with the oxygen combined in organic compounds and carbon dioxide. Photosynthetic organisms, using solar energy, generate dioxygen from water and liberate it into the atmosphere, while heterotrophic cells take up atmospheric dioxygen to oxidize organic compounds and thereby provide energy. *Compare* **carbon cycle**.

oxygen debt the oxygen deficit that develops when a normally aerobic organism or tissue cannot increase its oxygen uptake sufficiently to match a temporarily increased energy requirement, as in muscular exercise. After the increased energy requirement ceases, this deficit has to be made good by a continuing increased rate of oxygen uptake until normal aerobic metabolism is restored.

oxygen demand *see* **biochemical oxygen demand**, **chemical oxygen demand**.

oxygen electrode a device for measuring dioxygen activity in a liquid or gas. It consists essentially of a silver–silver chloride anode in saturated potassium chloride solution and a platinum or gold cathode. When an electric potential is applied between these electrodes dioxygen is electrolytically reduced at the cathode, the current flowing being proportional to the dioxygen activity when the applied potential is 0.5–0.8 V. The electrodes are either directly exposed to the sample or, in the **Clark electrode**, separated from it by a thin dioxygen-permeable membrane in order to prevent deposition of interfering substances on the cathode.

oxygen quotient *(sometimes)* the **metabolic quotient** with respect to dioxygen, *symbol*: Q_{O_2}.

oxyhemoglobin *symbol*: HbO_2; the fully oxygenated form of **hemoglobin**. It is bright red in colour and has a characteristic absorption spectrum.

oxyhydrogen reaction *an alternative name for* **knallgas reaction**.

oxymyoglobin *symbol*: MbO_2; the fully oxygenated form of **myoglobin**. It is bright red in colour and has a characteristic absorption spectrum.

oxyntic acid-secreting; applied especially to the hydrochloric acid-secreting parietal cells of the gastric mucosa.

oxyntomodulin *an alternative name for* glucagon-37; *see* **enteroglucagon**.

oxyproline *an older name for* **hydroxyproline**. *Compare* **5-oxoproline**.

oxysome *an alternative name for* **elementary particle** (def. 2).

oxytetracycline 5-hydroxytetracycline; an antibiotic that is similar in action to **tetracycline**. Proprietary names include Terramycin.

oxytocin *or (sometimes)* **ocytocin** *abbr.*: OXT; a heterodetic cyclic nonapeptide amide,

$$Cys^1\text{-}Tyr\text{-}Ile\text{-}Gln\text{-}Asn\text{-}Cys^6\text{-}Pro\text{-}Leu\text{-}Gly\text{-}NH_2$$

(Cys^1 and Cys^6 form a disulfide bond). It is one of the two (or possibly more) hormones secreted by the neurohypophysis of the pituitary gland. It facilitates the ejection of milk by stimulating the myoepithelial cells in the mammary gland, and it may also aid parturition by stimulating contraction of the uterus. It is synthesized as a polypeptide precursor that is cleaved to oxytocin and neurophysin 1 (for database code *see* **neurophysin**). Oxytocin was the first peptide hormone to be chemically synthesized. [*Note*: the spelling ocytocin is preferred on etymological grounds, the name being derived from the Greek *okytokos*, fast birth, rather than from the Greek *oxys*, acid, sharp; however, the spelling oxytocin is in wide use, esp. in the English language.] *See also* **vasopressin**.

oxytocin receptor any of a number of membrane proteins that bind oxytocin and mediate its intracellular effects. Structurally they are of the seven-transmembrane-domain type, characteristic of G-protein-coupled receptors, and activate the **phosphatidylinositol cycle**. Example from *Sus scrofa*: database code OXYR_PIG, 386 amino acids (42.52 kDa).

+oyl *suffix (in chemical nomenclature)* denoting conversion (of a mono- or dicarboxylic acid) to the corresponding mono- or divalent acyl group by removal of hydroxyl from the carboxyl group; e.g. the univalent acyl group, hexanoyl, CH_3–$[CH_2]_4$–CO–, is derived from hexanoic acid, CH_3–$[CH_2]_4$–COOH. It is used also when the carbonyl oxygen atom of the acyl group has been replaced by =NH, =N–NH_2, =N–OH, or =S. *See also* **+yl**.

oz *symbol for* ounce.

ozone *symbol*: O_3; trioxygen; a colourless, highly reactive gas present in the stratosphere, where it is formed under the influence of short-wavelength ultraviolet radiation. It is also normally present in trace amounts in air, and is formed by the action of sunlight on hydrocarbons and nitrogen oxides – present in vehicle emissions. The latter process can lead to harmful accumulations of ozone at or near ground level. In contrast, stratospheric ozone protects the biosphere from highly damaging ultraviolet radiation, especially UV-C.

ozonolysis a method used for locating a double bond in an alkene. The alkene is treated with ozone, and the resulting ozonide is then cleaved to form two carbonyl compounds, one from each moiety of the parent compound.

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Pp

p *symbol for* **1** pico+ (SI prefix denoting 10^{-12} times). **2** the negative logarithm to the base ten, as in pH, p*K*. **3** proton; it may be written as p^+ to indicate its charge. **4** a phosphoric residue (alternative to *P*). **5** the protein product of a gene; it is prefixed to the product's molecular mass to designate a particular entity, e.g. **p53**. **6** *(in atomic spectroscopy)* electron state $l = 1$.

p *symbol for* **1** pressure (alternative to *P*). **2** partial pressure of a gas. The gas may be specified by a subscript or in parentheses; e.g. p_{O_2} or $p(O_2)$. **3** pyranose form (in monosaccharide symbolism); e.g. Glc*p*, glucopyranose; Gal*p*A, galactopyranuronic acid. **4** pitch height (of a helix). **5** (bold italic) (electric) dipole moment (of a molecule), alternative to ***μ*** (bold italic). **6** (bold italic) momentum. **7** probability (alternative to *P*).

p- *prefix (in chemical nomenclature)* denoting ***para-***. *Compare* ***m-***, ***o-***.

p_{50} *symbol for* the partial pressure of a gas at which a binding protein is 50% saturated with it.

p_{LR} *symbol for* the proportion of receptors or binding sites occupied by ligand L.

p_{LR^*} *symbol for* the proportion of receptors in which ligand L occupies its binding site(s), and which are in an active state.

p_R *symbol for* the proportion of receptors or binding sites free of ligand.

P *symbol for* **1** peta+ (SI prefix denoting 10^{15} times). **2** poise. **3** phosphorus. **4** a residue of the α-amino (strictly, cyclic α-alkylamino) acid proline (alternative to Pro). *abbr. for* **5** phosphate or a phosphoric group, as in ATP. **6** *(in genetics)* parental generation. **7** a site near a peptidase cleavage site (*see* **peptidase P-site**).

P_i *symbol for* inorganic phosphate.

P *symbol for* **1** pressure (alternative to *p*). **2** radiant power (alternative to *Φ*). **3** probability (alternative to *p*). **4** parity (of a wave function).

p53 a 53 kDa nuclear phosphoprotein originally discovered attached to large T-antigen in cells transformed with **simian virus 40**. It is a probable human cell cycle regulator and *trans*-activator (*see* ***trans*-acting**) that acts negatively to regulate cellular division by controlling a set of genes required for this process; one of the genes activated is an inhibitor of **cyclin-dependent protein kinases**. p53 acts as a tumour suppressor in some (not all) tissues; mutations in the p53 gene are the most common genetic alterations in human cancers. Wild-type p53 can suppress or inhibit the transformation of cells in culture either by viral or cellular oncogenes, and introduction of wild-type cDNA into a transformed cell in culture stops growth. Hence the p53 gene is classed as a **tumour-suppressor gene**. Three functional domains of p53 have been defined: an N-terminal transcriptional activation domain (residues 1–42), a central DNA-binding domain (residues 120–290), and a C-terminal regulatory domain (residues 311–393). The DNA-binding domain recognizes a DNA motif in genes that are activated by p53, and mutations in p53 that are associated with human cancers generally cluster in its DNA-binding domain. Database code WT1_HUMAN, 449 amino acids (49.13 kDa).

P0 a **myelin protein**.

P1 a temperate bacteriophage whose natural hosts are *Shigella* spp. but which was used formerly for generalized transduction in *Escherichia coli* and is currently used as the basis for the **P1 cloning vector**, which can carry up to 100 kbp insert DNA. P1 prophage is a plasmid.

P2 a **myelin protein**.

P65 *see* **synaptotagmin I**.

P81 *see* **ezrin**.

P450 *or* **P-450** any of a group of widely occurring heme-containing proteins that embraces various separately classified enzymes. They are named from the location of the Soret band (*see* **cytochrome absorption bands**) of the reduced CO complex at 450 nm. The group includes unspecific monooxygenase (EC 1.14.14.1), camphor 5-monooxygenase (EC 1.14.15.1), alkane 1-monooxygenase (EC 1.14.15.3), steroid 11β-monooxygenase (EC 1.14.15.4), **cholesterol monooxygenase (side-chain-cleaving)** (EC 1.14.15.6), prostacyclin synthase (EC 5.3.99.4), **thromboxane-A synthase** (EC 5.3.99.5), and probably chloride peroxidase (EC 1.11.1.10). This type of enzyme is also known as **cytochrome P450** (see this for more detail) and considered as a *b*-type **cytochrome**. The name **heme-thiolate protein** has been proposed on the grounds of a thiolate ligand at the heme being responsible for the group's unusual spectral and catalytic properties.

P680 *or* **pigment 680** a type of chlorophyll *a*, having an absorption maximum at 680 nm, that constitutes the reaction centre of **photosystem** II in most species. It has a redox potential of >+0.81 V; the oxidized form, $P680^+$, is a powerful oxidant that can abstract electrons from water with the evolution of dioxygen. *See also* **chlorophyll**.

P700 *or* **pigment 700** a type of chlorophyll *a*, having an absorption maximum at 700 nm, that constitutes the reaction centre of **photosystem** I. It has a redox potential of approximately +0.5 V, its electron being used ultimately to reduce NADP via ferredoxin. *See also* **chlorophyll**.

P870 the special pair of bacteriochlorophyll *a* in the **photosynthetic reaction centre** of bacteria, so named because they have an absorption maximum of 870 nm.

P960 the special pair of bacteriochlorophyll *b* in the **photosynthetic reaction centre** of bacteria, so named because they have an absorption maximum of 960 nm.

Pa *symbol for* pascal.

pA_2 the negative logarithm to the base 10 of the molar concentration of antagonist that makes it necessary to double the concentration of agonist needed to elicit the original submaximal response.

$p[A]_{50}$ the negative logarithm to the base 10 of the **$[A]_{50}$** of an agonist. pEC_{50} is the corresponding term for the **EC_{50}** of an agonist (often used interchangeably with $[A]_{50}$).

PAB *or* **PABA** *abbr. for para*-aminobenzoate; *para*-aminobenzoic acid. *See* ***p*-aminobenzoic acid**.

PABA test an indirect test of pancreatic function in which the synthetic peptide *N*-benzoyl-L-tyrosyl-*p*-aminobenzoic acid (BT-PABA) is administered orally, usually with a small amount of [^{14}C]-*p*-aminobenzoic acid (PABA). Normally the peptide is hydrolysed by chymotrypsin to PABA, which is absorbed and excreted in the urine, but in pancreatic insufficiency hydrolysis is much reduced.

pacemaker reaction any metabolic reaction whose rate depends on factors other than the amounts of enzyme or substrate. An enzyme catalysing such a reaction may be termed a **pacemaker enzyme**.

pachyman *see* **callose**.

pachytene the third phase of prophase I in **meiosis**.

package **1** *(in cell biology)* to surround (one or a number of macromolecules) with a membrane in the formation of a mature secretory granule. **2** *(in virology)* to enclose the nucleic-acid core of a virus particle with a protein shell (the capsid) to form a mature virion; to encapsidate.

packing *(in chromatography)* the material (whether active solid, liquid held on solid support, or swollen gel) that is introduced into a column and that consists of or contains what is to become the stationary phase during a chromatographic separation.

packing density the ratio of the minimum (or actual) volume of an object, such as a molecule in a crystal or in solution, to the total volume it occupies. For a macromolecule or region of

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a macromolecule, it is the ratio of the volume enclosed by the van der Waals envelope of all atoms in the molecule or region to the total volume of the molecule or region. Theoretical values are 0.74 for close-packed spheres, 0.91 for infinite cylinders, and 1.0 for a continuous solid.

packing fraction the ratio of the relative atomic mass of a particular nuclide minus its nucleon number divided by its nucleon number. It is positive for the lightest and heaviest nuclides and negative for nuclides of intermediate mass.

Paclitaxel *a proprietary name for* **taxol**.

PAF *abbr. for* platelet-activating factor.

PAGE *abbr. for* polyacrylamide gel electrophoresis.

PAGIF *abbr. for* polyacrylamide gel isoelectric focusing. *See* **polyacrylamide gel electrophoresis**.

PAH *abbr. for para*-aminohippurate; *para*-aminohippuric acid.

pair *see* **base pair**.

paired the gene for a sequence-specific DNA-binding homeobox segmentation protein in *Drosophila melanogaster*. It is one of a number of **pair-rule genes**, each of which specifies a simple alternation with a repeat distance of two segments. Their protein products are characterized by four motifs, referred to as the paired box. Example from *D. melanogaster*: database code HMPR_DROME, 613 amino acids (65.43 kDa).

paired box *see* ***paired***, ***Pax*** **genes**.

pair-rule gene *see* ***paired***.

PaJaMa experiment *the nickname for* a bacterial mating experiment carried out at l'Institut Pasteur, Paris, that showed that induction and repression of the enzyme β-galactosidase in *Escherichia coli* are regulated by two closely linked genes, one of which produces a cytoplasmic repressing substance that blocks the expression of the other. [From the names of the experimenters: Pardee, **Jacob**, and **Monod**.]

Palade, George Emil (1912–), Romanian-born US cell biologist; Nobel Laureate in Physiology or Medicine (1974) jointly with A. Claude and C. R. M. J. de Duve 'for their discoveries concerning the structural and functional organization of the cell.'

palindrome **1** any linear arrangement of symbols, such as letters or digits, that has the same sequence from either end; e.g. noon, radar; 75311357; 'Madam, in Eden I'm Adam'. **2** *(in molecular biology) or* **palindromic sequence** *a popular name for* a DNA sequence with a twofold rotational axis of symmetry (**dyad symmetry**). Confusingly the term is used in at least two distinguishable senses: (1) to describe a region of local twofold rotational symmetry in duplex DNA, e.g.

5′-GAATTC-3′
3′-CTTAAG-5′

and (2) to describe a sequence in a single polynucleotide strand that contains an inverted repeat, e.g. 5′-TGA-AGT-3′. It is also sometimes applied to a region of either a single- or a double-stranded polynucleotide that is capable of forming one or more **hairpins** containing palindromes of the first type; an example is shown at **cruciform**. Examples of palindromes are **operators** and **restriction sites** but, in general, any stem–loop in RNA must have a corresponding palindrome in the DNA from which the RNA was transcribed. —**palindromic** *adj.*

pallidin any of a group of endogenous carbohydrate-binding proteins (**lectins**) produced by cells of the slime mould *Polysphondylium pallidum* during differentiation. Similar to **discoidin**, they may be concerned in cell adhesion.

palmitate **1** *numerical symbol*: 16:0; *the trivial name for* hexadecanoate, $CH_3–[CH_2]_{14}–COO^-$, the anion derived from palmitic acid (i.e. hexadecanoic acid), a saturated straight-chain higher fatty acid. **2** any mixture of free palmitic acid and its anion. **3** any salt or ester of hexadecanoic acid. *See also* **palmitoyl**.

palmitate synthase *see* **fatty-acid synthase complex**.

palmitic acid hexadecanoic acid; a saturated straight-chain fatty acid having sixteen carbon atoms per molecule, and a major component of plant and animal fats. *See* **palmitate**.

palmitoleate **1** *numerical symbol*: 16:1(9); *the trivial name for* (*Z*)-hexadec-9-enoate, $CH_3–[CH_2]_5–CH=CH–[CH_2]_7–COO^-$, the anion derived from palmitoleic acid, (*Z*)-hexadec-9-enoic acid, a monounsaturated straight-chain higher fatty acid. **2** any mixture of free palmitoleic acid and its anion. **3** any salt or ester of 9-hexadecenoic acid. *See also* **palmitoleoyl**.

palmitoleic family (of polyunsaturated fatty acids) a series of polyenoic acids in which the hydrocarbon chain terminates with the alkenyl grouping $CH_3–[CH_2]_5–CH=CH–$ (as in palmitoleic acid (*see* **palmitoleate**)); there are three other series of such acids, i.e. the **linoleic family**, **linolenic family**, and **oleic family**. Members of the palmitoleic family can be synthesized from palmitic acid via palmitoleic acid by chain elongation and/or desaturation, but in mammals not from linoleic, (9,12,15)-linolenic, or oleic acids; the series includes *cis*-vaccenic acid.

palmitoleoyl *symbol*: ΔPam; *the trivial name for* (*Z*)-hexadec-9-enoyl, $CH_3–[CH_2]_5–CH=CH–[CH_2]_7–CO–$ (*cis* isomer), the acyl group derived from palmitoleic acid (i.e. (*Z*)-hexadec-9-enoic acid). It is a relatively minor component of plant and animal lipids. The chain is synthesized metabolically by the action of a Δ^9-desaturase on palmitoyl-CoA.

palmitoyl *symbol*: Pam; *the trivial name for* hexadecanoyl, $CH_3–[CH_2]_{14}–CO–$, the acyl group derived from palmitic acid (i.e. hexadecanoic acid). This is one of the major fatty-acid components of plant and animal lipids; together with stearic acid it represents a high proportion (often around 30%) of the fatty-acid content of dietary and other lipids. It acts as a precursor in mammals for a family of unsaturated fatty acids in which all double bonds are nine or more carbons from the methyl terminus. The chain is synthesized metabolically from acetyl-CoA as palmitate (in mammals) or palmitoyl-CoA (in yeast), the product of fatty-acid synthase. See **fatty-acid synthase complex**.

palmityl **1** *or* **cetyl** *a common name for* hexadecyl, $CH_3–[CH_2]_{14}–CH_2–$, the alkyl group derived from hexadecane. **2** *a former name (now incorrect) for* **palmitoyl**.

palytoxin any of a group of structurally very similar potent neurotoxins isolated from the marine zoanthid *Palythoa toxica* or other *Palythoa* spp. Each consists of a single carbon chain of 115 carbon atoms containing 64 chiral centres and seven double bonds, and terminating in nitrogen-containing groups; there are 128 carbons in all and a further double bond in a methylene group. The chain bears numerous hydroxyl groups and a number of methyl groups, and in several places it is folded and formed into pyran rings. Palytoxin is the most deadly nonproteinaceous material isolated, having 50 times the toxicity of **tetrodotoxin** in mice. The number of stereoisomers is 2^{64} = 18 446 744 073 709 551 620 (not including possible *E*/*Z* variations at the double bonds!).

Pam *symbol for* **palmitoyl** (i.e. hexadecanoyl).

pancreas a compound gland, occurring in the abdominal cavity of most vertebrates, that has both exocrine and endocrine functions. The major (exocrine) part consists of acinar tissue, which secretes **pancreatic juice** into the upper part of the gut (duodenum in mammals). Within this acinar tissue are scattered numerous (endocrine) **islets of Langerhans**, containing notably A cells, secreting **glucagon**, B cells, secreting **insulin**, and D cells, secreting **somatostatin**. —**pancreatic** *adj.*

pancreastatin a 49-residue peptide hormone that acts as an inhibitor of glucose-induced insulin release from the pancreas. It also inhibits exocrine pancreatic excretion. It was originally isolated from porcine pancreas, where it is colocalized with insulin, glucagon and somatostatin, but is synthesized as part of the sequence of **chromogranin** A and is thus found in tissues where the chromogranin gene is expressed, including most endocrine cells.

pancreatic cholera *an alternative name for* **Verner–Morrison syndrome**.

pancreatic diabetes *an older term for* insulin-dependent **diabetes mellitus**.

pancreatic hormone *or* **pancreatic polypeptide** *abbr.*: PP; a

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crystallizable polypeptide present in the **PP cells** of the pancreas, first detected as an impurity in insulin preparations. Avian pancreatic polypeptide, known as aPP, has been isolated from chicken and turkey pancreas; bovine, human, ovine, and porcine homologues, known as bPP, hPP, oPP, and pPP, respectively, have also been identified. All have 36 amino-acid residues with C-terminal tyrosinamide and show considerable sequence homologies. The PP level in the plasma rises rapidly after feeding, especially with protein foods; the hormone appears to act as a regulator of pancreatic and gastrointestinal functions; sequence from human: APLEPVYPGDNATPEQMAQYAADLRRYINMLTRPRY(NH_2); database code (precursor) PAHO_HUMAN, 95 amino acids (10.43 kDa) also contains an icosapeptide of uncertain physiological role (residues 69–88).

pancreatic islet *an alternative name for* **islet of Langerhans**.

pancreatic juice a slightly alkaline digestive juice secreted by the exocrine pancreas into the upper part of the small intestine. It contains numerous enzymes and inactive enzyme precursors including **a-amylase**, chymotrypsinogen, **lipase**, procarboxypeptidase, proelastase, prophospholipase A_2, ribonuclease, and trypsinogen. Its high concentration of hydrogencarbonate ions helps to neutralize the acid digesta from the stomach.

pancreatic lipase a Ca^{2+}-requiring triacylglycerol lipase (EC 3.1.1.3) that is secreted into the intestine by the exocrine pancreas when this is stimulated by cholecystokinin in response to ingestion of food. Its role is to degrade triacylglycerols, partially or completely, to fatty acids and glycerol in the intestine; it acts at an ester–water interface. It is a glycoprotein with sequence similarity with other lipases. Example (precursor) from human: database code LIPP_HUMAN, 465 amino acids (51.10 kDa).

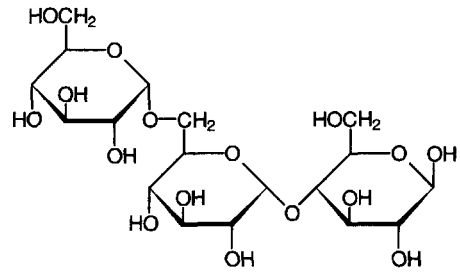
pancreatic polypeptide *abbr.*: PP; *another name for* **pancreatic hormone**.

pancreatic thread protein *or* **pancreatic stone protein** (*abbr.*: PSP); a C-type lectin that may inhibit spontaneous calcium carbonate precipitation, and one of the major secretory proteins of the human exocrine pancreas. It is found in acinar cells of pancreas and (in smaller amounts) in the brain. It is a major soluble protein of human pancreatic calculi and a Ca^{2+}-binding phosphoprotein present in zymogen granules of pancreatic acinar cells and secreted in pancreatic juice of normal subjects and calculus formers. It inhibits calcium carbonate precipitation from the juice. The protein is rich in aromatic amino acids. Between pH 5.4 and 9.2 it undergoes reversible fibril formation. It is also typically characteristic of infant brains. There is increased expression of PSP-like proteins in Down's syndrome and Alzheimer's disease. Example (precursor) from human: database code LITH_HUMAN, 166 amino acids (18.71 kDa).

pancreatic trypsin inhibitor *abbr.*: PTI; a serine proteinase inhibitor, *correctly known as* **pancreatic secretory trypsin inhibitor**. A crystallizable protein trypsin inhibitor isolated from bovine pancreas, it forms a crystalline complex with trypsin and is relatively heat-stable in trichloroacetic acid solution. Its physiological role is to control trypsin activation of zymogens. The bovine protein is of known sequence: NILGREAKCTNEVNGCPRIYNPVCGTDGVTYSNECLLCMENKERQTPVLIQKSGPC. The 3-D structure is also known, and it is a favoured model for testing protein-folding algorithms. Example (bovine): database code IPST_BOVIN, 56 amino acids (6.16 kDa). It was also formerly known as **Kunitz and Northrop inhibitor**.

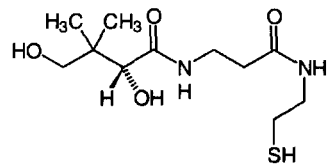
pancreozymin *abbr.*: PZ; a putative hormone having secretagogic activity on the exocrine pancreas and extractable from duodenal mucosa. It is now known to be identical with **cholecystokinin**.

panose an oligosaccharide, Glc(α1-6)Glc(α1-4)Glc; it is found in the fungus *Aspergillus niger*.

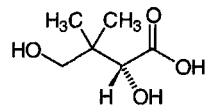


panose

pantetheine *N*-pantothenylcysteamine; the D-enantiomer is a growth factor for *Lactobacillus bulgaricus*, and is an intermediate in the pathway for the biosynthesis of coenzyme A in mammalian liver and some microorganisms.

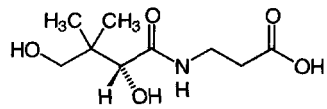


pantoate **1** the anion, HO–CH_2–$C(CH_3)_2$–CH(OH)–COO^-, derived from pantoic acid (i.e. (*R*)-2,4-dihydroxy-3,3-dimethylbutyric acid). **2** any salt or ester of pantoic acid.



pantoic acid

pantothenate **1** the anion, HO–CH_2–$C(CH_3)_2$–CH(OH)–CO–NH–CH_2–CH_2–COO^- (i.e. *N*-pantoyl-β-alanine anion), derived from pantothenic acid, a **B** vitamin complex; only the D-(*R*)-enantiomer is biologically active. **2** any salt of pantothenic acid.



pantothenic acid

pantothenyl the acyl group, HO–CH_2–$C(CH_3)_2$–CH(OH)–CO–NH–CH_2–CH_2–CO–, derived from pantothenic acid; coenzyme A is a D-(*R*)-pantothenyl derivative.

pantoyl **1** the acyl group, HO–CH_2–$C(CH_3)_2$–CH(OH)–CO–, derived from pantoic acid, 2,4-dihydroxy-3,3-dimethylbutyric acid.

PAP *abbr. for* peroxidase–antiperoxidase.

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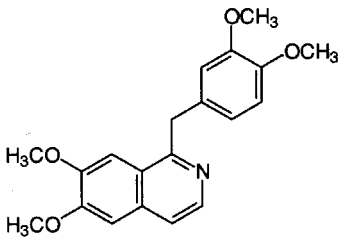
papain *or* **papaya peptidase I** EC 3.4.22.2; a cysteine endopeptidase obtained from the latex, leaves, and unripe fruit of the papaya (or pawpaw) tree, *Carica papaya*. It will preferentially hydrolyse peptide bonds at the carbonyl end of Arg, Lys, and Phe residues (but never Val), with preference for large hydrophobic residues at the P2 position. It also has esterase, thiolesterase, transamidase, and transesterase activity. Papain is unusually stable to elevated temperatures and to denaturing agents and consists of a single polypeptide chain of 212 amino-acid residues. Example from *C. papaya*: database code NRL_1PPD, 212 amino acids (23.40 kDa); 3-D structure known; α and β regions.

papaverine 1-[(3,4-dimethoxyphenyl)methyl]-6,7-dimethoxyisoquinoline; a constituent of **opium** that acts as a smooth muscle relaxant; this action is thought to be due to phosphodiesterase inhibitory activity and blockade of membrane calcium channels.



paper chromatogram the visible result of a chromatographic separation effected on paper.

paper chromatography *abbr.*: PC; a technique of **chromatography**, applicable to microgram quantities of soluble substances, in which specially prepared filter paper, **chromatography paper**, forms the support for the stationary phase. The latter is commonly a film of water held by adsorption on the cellulose fibres of the paper and in equilibrium with a water-immiscible liquid or liquid mixture, which forms the mobile phase. A solution of a sample is applied near one end of a strip of paper, allowed to dry, and the mobile phase allowed to flow over the strip from that end. If the sample consists of only one component, development using an appropriate method of detection will reveal a single spot at a characteristic distance from the origin relative to that travelled by the mobile phase; in general, a mixture will give rise to a number of spots each occupying a different and characteristic position. Separations occur essentially by partition between the mobile and stationary phases, with some contribution, under certain conditions, attributable to adsorption or ion-exchange onto the paper support. An elaboration of the technique uses a square of paper on which two successive separations are effected at right-angles using mobile phases of differing separatory powers to produce a two-dimensional pattern of spots on the paper. With suitable treatment of the paper and an appropriate choice of the composition of the two phases, reversed-phase partition chromatography on paper may be effected. Since cellulose is chiral, some enantiomer separations are possible.

paper electrophoresis a type of **zone electrophoresis** on (filter) paper.

Papovaviridae a family of DNA viruses, most or all of which are, under suitable conditions, oncogenic in vertebrate hosts. The virion, 45–55 nm in diameter, consists of a nonenveloped icosahedral capsid with 72 capsomeres, and contains a circular DNA genome.

papovavirus any virus belonging to the family **Papovaviridae**. The name derives from papilloma, polyoma, and vacuolating agent, an early name for **simian virus 40**.

PAPS *abbr. for* 3′-phosphoadenosine-5′-phosphosulfate; i.e. adenosine 3′-phosphate 5′-phosphosulfate.

par+ *a variant form of* **para+** (before a vowel).

para 1 characterized by or relating to (substitution at) two ring-carbon atoms separated by two others in a monocyclic aromatic compound. 2 *(followed by* to) at a position in a benzene ring next but two to a particular (specified) substituent. *See also* ***para-***.

para+ *or (before a vowel)* **par+** *prefix* indicating beside or near; beyond; resembling; defective or abnormal.

para- *abbr.*: *p-*; *prefix (in chemical nomenclature)* denoting an isomer of a disubstituted monocyclic aromatic compound in which the substituents are attached at positions 1 and 4 of the ring. *Compare* ***meta-***, ***ortho-***.

parabiont either individual of a pair united in **parabiosis**.

parabiosis the state or condition of two individual animals being functionally united, either naturally, as in Siamese twins, or as a result of an experimental procedure. —**parabiotic** *adj.*

paracasein *an alternative name (esp. US) for* **casein** (def. 2).

paracetamol *see* **acetaminophen**.

paracrine 1 describing or relating to a regulatory cell that secretes an agonist into intercellular spaces in which it diffuses to a target cell other than that which produces it; describing or relating to such an agonist. 2 such an agonist; a **paramone**. *Compare* **endocrine**, **neurocrine**, **neuroendocrine**.

paracrystal any assemblage of molecules or particles having a certain degree of order but one that is insufficient for it to be considered a true crystal. —**paracrystalline** *adj.*; **paracrystallinity** *n.*

paradaxin *or* **pardaxin** any of several ichthyotoxic, neurotoxic peptides, isolated from the defence secretion of the Red Sea Moses sole fish, *Paradachirus marmoratus*, or the Pacific sole, *Paradachirus pavoninus*, that act as a shark repellent. Each consists of 33 amino acids, with hydrophilic C-terminal and hydrophobic N-terminal regions and with physical and pharmacological similarities with **melittin** but no sequence homology. Example, paradaxin P-2 from *P. pavoninus*: database code PAP2_PARPV, 33 amino acids (3.32 kDa).

paraffin 1 *an obsolete term for* **alkane**. 2 *or* **paraffin oil** *or* **kerosene** *or* **kerosine** any liquid mixture, consisting mainly of alkanes, with a boiling point range of 150–300 °C and relative density range of 0.78–0.82. 3 *an alternative name for* **paraffin wax**. *Compare* **liquid paraffin**.

paraffin wax any waxy mixture of higher alkanes, obtained as a residue from the distillation of petroleum, with a relative density of ≈0.9 and a melting point range of 45–65 °C.

Parafilm *the proprietary name for* a flexible, moisture-proof, thermoplastic tissue useful for temporarily sealing small containers.

parafollicular cell *an alternative name for* **C cell** (when found in the thyroid gland).

parafusin an evolutionarily conserved phosphoglycoprotein involved in exocytosis. It is rapidly dephosphorylated via a Ca^{2+}-dependent process when secretagogues induce exocytosis in competent cells. Example from *Paramecium tetraurelia*: database code PARPARAFUS, 475 amino acids (52.94 kDa).

parahematin *or (esp. Brit.)* **parahaematin** *a former name for* **ferrihemochrome**.

parallel 1 *(in biochemistry)* describing a pair of linear structures, such as two polynucleotide or polypeptide chains, that are polarized or asymmetric in the same direction. 2 *(in physical chemistry)* denoting the spins of a pair of electrons, occupying the same atomic or molecular orbital, that are described by the same spin quantum number. *Compare* **antiparallel**. 3 *(in electricity)* describing an electrical component that is connected to the same two points in a circuit as another component; describing two or more components that are so connected.

parallel dichroism *see* **dichroic ratio**.

parallelism the quality or state of being parallel; similarity in corresponding details or in evolutionary pattern.

paramagnetism the property displayed by substances that have a positive but small magnetic susceptibility, due to the presence in them of atoms with permanent magnetic dipoles

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caused by unpaired electron spins (with a contribution from the orbital motion of the electrons). These dipoles tend to align themselves in the direction of an applied magnetic field but no permanent magnetism is conferred on such substances. *Compare* **diamagnetism**, **ferromagnetism**. —**paramagnetic** *adj.*

paramecium (*pl.* **paramecia**) any freshwater protozoan belonging to the genus *Paramecium*. Typically 50–300 μm in length, they are ovoid and uniformly ciliated. *See also* **kappa particle**.

parameter **1** *(in mathematics)* an unknown quantity that is a constant in a particular context but that may have different values in other (similar) contexts; e.g. the coefficient b in the general equation, $y = bx + c$, representing a family of straight lines. **2** *(in statistics)* a numerical characteristic of a population (as opposed to that of a sample of such a population). **3** any distinguishing characteristic of something, especially one to which a measured value is or can be ascribed. —**parametric** *adj.*

paramomycin an aminoglycoside antibiotic produced by *Streptomyces paromomycinus*. Its actions are similar to those of **neomycin**.

paramone *a proposed name for* **paracrine** agonist, derived as a contraction of 'paracrine hormone'.

paramylon a storage polysaccharide occurring in *Euglena gracilis*. It comprises a backbone of $\beta1\rightarrow3$-glucopyranose units with side chains joined by $\alpha1\rightarrow6$ linkages.

paramyosin a two-chain, coiled-coil, α-helical ≈200 kDa protein that forms the core protein of the thick filaments of a number of invertebrate muscles.

paramyxovirus any of a group of RNA animal viruses of the family Paramyxoviridae (distinguish from the genus Paramyxovirus), in class V of the **Baltimore classification**, consisting of enveloped, pleomorphic particles ≈150 nm in diameter with helical nucleocapsids, 1000 nm long and 18 nm in diameter. They contain single-stranded RNA (minus strand) of 7 MDa plus virion polymerase. The group includes viruses causing mumps, measles, Newcastle disease of chickens, and distemper of dogs, and the morbilliviruses, pneumoviruses, and parainfluenza viruses.

paranemic describing the nature of the coiling of a double-stranded helix in which the two strands are not intertwined, i.e. they may be separated without uncoiling. *Compare* **plectonemic**.

parapepsin I *an alternative name for* **pepsin B**.

parapepsin II *an alternative name for* porcine **gastricsin** (i.e. pepsin C).

paraprotein *name originally given to* any plasma protein that gave an abnormal band on electrophoresis, derived from **para+** + protein. Usually such a protein is a monoclonal immunoglobulin derived from neoplastic plasma cells and present at abnormally high concentration in the blood plasma. Such proteins are seen as a discrete band in the gamma-globulin region, but they may appear elsewhere if the paraprotein is IgA or IgM. Examples are proteins characteristic of a **myeloma**, e.g. **Bence-Jones protein**, amyloid proteins, **Waldenstrom's macroglobulinemia**, or cryoglobulins. Some paraproteins are not abnormal, e.g. the immunoglobulin that arises as a result of a severe bacterial infection.

paraproteinemia *or (esp. Brit.)* **paraproteinaemia** the presence in blood plasma of **paraprotein**.

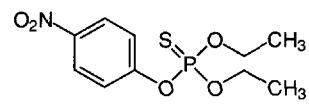
Paraquat methyl viologen; 1,1′-dimethyl-4,4′-bipyridynium dichloride; a nonselective herbicide whose action requires direct contact with the plant. It is highly toxic to humans and other animals if ingested in undiluted form.

parasite any organism that spends all or part of its life cycle in (**endoparasite**) or on (**ectoparasite**) another living organism of a different species (its **host**), from which it obtains nourishment and/or protection, and to which it is usually detrimental. *Compare* **symbiont**.

parastatin a 73-amino-acid peptide hormone, M_r 11 000, that inhibits **parathyrin** secretion. Porcine parastatin has the amino-acid sequence: LSFRAPAYGFRGPGLQLRRGWRPSSRED-SVEAGLPLQVRXYLEEKKEEEGSANRRPEDQELESLSAI-EAELEK. Activity resides in a 19-amino-acid N-terminal fragment; that from rat has the sequence: LSFRARAYGF-RDPGPQLRR. It is synthesized as part of the sequence of **chromogranin** A.

paratartaric acid *an old name for* racemic (DL)-tartaric acid. The resolution of this acid into the D- and L-enantiomers by Pasteur was a landmark experiment in stereochemistry. *See* **tartaric acid**.

parathion *O*,*O*-diethyl *O*-*p*-nitrophenyl phosphorothioate; a compound that acts as an inhibitor of cholinesterase through covalent bonding to the esteratic site of the enzyme. It is used as a chemical warfare agent and insecticide.



Parathormone *a proprietary name for* **parathyrin**.

parathyrin *or* **parathyroid hormone** (*abbr.*: PTH); a 9.5 kDa polypeptide hormone, consisting of a single chain of 83 amino-acid residues (bovine). It is synthesized in parathyroid tissue by proteolysis of a 12.5 kDa prohormone. Parathyrin acts in conjunction with **calcitonin** and other hormones to control calcium and phosphate metabolism; it elevates the blood calcium level by dissolving the salts in bone and preventing their renal excretion. Example (precursor) from human: database code PTHY_HUMAN, 115 amino acids (12.85 kDa). *Proprietary name*: Parathormone.

parathyroid **1** situated near the thyroid gland. **2** of, pertaining to, or produced by the parathyroid gland. **3** the parathyroid gland.

parathyroid gland an endocrine gland of higher vertebrates; there are typically two pairs, located near or within the thyroid. They develop from the gill pouches, and secrete **parathyrin**.

parathyroid hormone *abbr.*: PTH; *an alternative name for* **parathyrin**.

paratope the part of an antibody, formed by the hypervariable loops of the **variable regions**, that binds to an **epitope**.

paratose 3,6-dideoxy-D-glucose; 3,6-dideoxy-D-*ribo*-hexose; a monosaccharide that occurs in type A O-antigen chains of the lipopolysaccharide on the outer membrane of certain species of *Salmonella*.

Parazoa a subkingdom of multicellular invertebrate animals comprising the sponges (phylum Porifera).

parenchyma **1** *(in botany)* in higher plants, any soft tissue consisting of thin-walled, relatively undifferentiated living cells. **2** *(in zoology)* the tissue constituting the essential or specialized part of an organ, as distinct from supportive tissue, blood vessels, etc. —**parenchymal** *adj.*; **parenchymatous** *adj.*

parenchymal liver cell *see* **hepatocyte**.

parent **1** any organism that has given rise to another such organism, whether sexually or asexually. **2** a precursor of some derived entity; applied, e.g., to a cell, a virus, a chromosome or molecule of DNA, or a radionuclide. **3** **parent compound** *(in chemical nomenclature)* the member of a group of related compounds that has the simplest chemical structure and that forms the basis for naming the others. —**parental** *adj.*

parenteral **1** located or occurring outside the intestine. **2** any route other than via the gastrointestinal tract, especially by injection. —**parenterally** *adv.*

parietal **1** of, pertaining to, or forming part of the wall of a body cavity or similar structure; e.g. the hydrochloric-acid-secreting **parietal cells** of the gastric mucosa, also known as oxyntic cells. **2** of or relating to the parietal bones of the skull.

parietal layer *see* **serous membrane**.

parinaric acid any octadeca-9,11,13,15-tetraenoic acid; two isomers are found in *Parinarium laurinum*, namely the (9*Z*,11*E*,13*E*,15*Z*)-isomer (α- or *cis*-parinaric acid) and the

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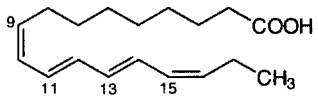
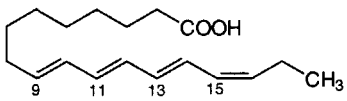
(9*E*,11*E*,13*E*,15*Z*)-isomer (β- or *trans*-parinaric acid). Both are useful as probes in membrane studies, *trans*-parinaric acid especially, as it partitions preferentially into the less fluid regions of membrane lipids with increased quantum yield. They inhibit neutrophil elastase.



α-parinaric acid



β-parinaric acid

Parkinson's disease *or* **parkinsonism** a progressive disorder of the central nervous system characterized by tremor and impaired muscular coordination, thought to be due to defective dopaminergic transmission in some parts of the brain. There is a loss of dopaminergic neurons connecting the substantia nigra with the striatum, resulting in loss of dopaminergic inhibition in the striatum, with resulting cholinergic hyperactivity. Therapy is aimed at replacement of dopamine, achieved by administration of L-**dopa**, which is converted to dopamine within the brain (dopamine itself does not cross the blood–brain barrier). *See also* **MPTP**. [After James Parkinson (1755–1824), British palaeontologist and surgeon, who first described the disease in 1817.]

Park nucleotide UDP-*N*-acetylmuramyl pentapeptide; an intermediate in the biosynthesis of peptidoglycan in the cell walls of most bacteria. [After James Theodore Park (1922–).]

parotid gland either of a pair of **salivary glands** situated near each ear in mammals. The duct runs forwards and empties into the oral cavity.

PARP *abbr. for* **1** procyclin. **2** proline/arginine-rich protein.

parsimony **1** *(in computing)* an algorithm used for determining sequence relationships in macromolecules. **2** *(in genetics)* the construction of evolutionary trees from protein and nucleic-acid sequences. It maximizes the genetic likeness associated with common ancestry, whilst minimizing the incidence of convergent mutation, and provides a way to find the best genealogical hypothesis from sequence data.

parthenocarpy the formation of fruit without the setting of seeds. It occurs naturally, but can be induced by spraying flowers with gibberellic acid (*see* **gibberellin**) to produce crops of seedless fruit.

parthenogenesis the development of a new individual from an unfertilized female gamete. —**parthenogenetic** *adj.*; **parthenogenetically** *adv.*

partial agonist an agonist that is unable to evoke the maximal response of a biological system, even at a concentrations sufficient to saturate the specific receptors.

partial derivative *(in mathematics)* the derivative of an expression containing two or more independent variables that is obtained by differentiating the expression with respect to only one of them, the remaining variable or variables being considered constant.

partial hydrolysate any mixture of monomers and oligomers resulting from a limited degree of chemical hydrolysis of a biopolymer or from its exposure to a specific hydrolytic enzyme.

partial inhibition *(sometimes)* a type of nonlinear enzyme inhibition in which saturation of the enzyme with inhibitor does not decrease the rate of the enzyme-catalysed reaction to zero.

partial inverse agonist an **inverse agonist** that evokes a submaximal response in a biological system, even at a concentration sufficient to saturate the specific receptors. At high concentrations it will diminish the actions of a full inverse agonist. *Compare* **antagonist**, **partial agonist**.

partially overlapping code *see* **overlapping code**.

partially overlapping gene *see* **overlapping gene**.

partial molar quantity a function of any particular extensive property (e.g. enthalpy, entropy, Gibbs energy, heat capacity, internal energy, volume) of a specified component of a single-phase multicomponent system that describes how that property varies, at constant pressure and temperature, with variation of the concentration of the component when the change in the property is expressed per mole of the component. Partial molar Gibbs energy is more usually known as **chemical potential**. *Compare* **partial specific quantity**.

partial pressure *symbol*: p_B *or* $p(B)$ (for a gas B); the pressure exerted by one particular gas in a mixture of nonreacting gases. It is defined as the pressure the gas would exert if it alone were present and occupied the whole volume of the mixture at the same temperature, and is equal to the product of the amount-of-substance fraction of the gaseous component in question and the total pressure of the gaseous system. *Compare* **tension**. *See also* p_{50}.

partial pressures, law of *see* **Dalton's law of partial pressures**.

partial specific quantity a function of any particular extensive property (e.g. enthalpy, entropy, Gibbs energy, heat capacity, internal energy, volume) of a specified component of a single-phase multicomponent system that describes how that property varies, at constant pressure and temperature, with variation of the concentration of the component when the change in the property is expressed per unit mass of the component. *Compare* **partial molar quantity**.

partial specific volume (of a solute) *symbol*: $\tilde{v}_B$; an instance of a **partial specific quantity**, defined as the change in volume of a solution on addition of a small amount of a solute B, expressed per unit mass of added solute and extrapolated to infinite dilution. The cgs unit (in which values are often listed) is $cm^3\ g^{-1}$ and the SI unit is $m^3\ kg^{-1}$.

particle **1** an extremely small piece or portion of (esp. solid or colloidal) matter. **2** **elementary particle**. —**particulate** *adj.*

particulate enzyme any enzyme that is bound to an insoluble cellular or subcellular structure or that has been artefactually or artificially attached to particulate material.

particulate radiation any form of radiation consisting of a stream of particles, especially alpha radiation, beta radiation, or neutron radiation emanating from a radioactive source.

partition **1** *(in chemistry)* *or* **distribution** the equilibration of a solute between two phases (usually of differing composition); the result of such a process. **2** *(in genetics)* the events that lead to the separation of chromosomes or to the segregation of plasmids into daughter cells in prokaryotic organisms.

partition chromatography any form of chromatography in which separation of the components of a mixture is based mainly on differences between the solubilities of the components in the stationary phase (in gas chromatography) or on differences between the solubilities of the components in the mobile and stationary phases (in liquid chromatography).

partition coefficient *or* **distribution coefficient** *symbol*: α *or* K_D; the ratio of the equilibrium concentrations of a pure substance dissolved in two phases that are in contact, at a specified temperature. The partition coefficient is independent of the concentrations provided that no chemical interaction occurs with either (or both) of the phases and that the presence of the solute does not affect their immiscibility.

partition function *symbol*: Z; a dimensionless mathematical function, derived by the application of statistical mechanical theory, that can be used to derive the average distribution of

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the internal energy of a system in terms of its partition between all its molecular inhabitants.

partition law *or* **distribution law** the principle that a solute, when added to a system consisting of two phases, will, at a given temperature, distribute itself between the two phases in proportion to its solubility in each of the two phases separately. **Henry's law** is a particular case of the partition law. *See also* **Nernst distribution law**.

parturition the act or process of giving birth to offspring.

parvalbumin any of a group of closely related ≈12 kDa muscle proteins that bind calcium ions. Parvalbumin α is a muscle **EF-hand** Ca^{2+}-binding protein, that may be involved in muscle relaxation. Example from human: database code PRVA-HUMAN, 109 amino acids (11.93 kDa). Parvalbumin β is known as **oncomodulin**.

parvovirus any of a group of small, animal viruses, in class II of the **Baltimore classification**, consisting of a naked capsid, 20–25 nm in diameter, and containing linear, single-stranded DNA of 1.2–1.8 MDa. Parvoviruses are highly resistant to chemical and physical agents.

parvulin a **peptidylprolyl isomerase** isolated from *Escherichia coli*. It does not have any function as an **immunophilin**. Database code CYPC_ECOLI, 92 amino acids (10.10 kDa).

PAS *abbr. for* **1** *p*-aminosalicylic acid. **2** periodic acid–Schiff; *see* **periodic acid–Schiff reaction**.

pascal *symbol*: Pa; the SI derived unit of pressure or stress. It is equal to a force of one newton per square metre; i.e.

$$1\ \text{Pa} = 1\ \text{N m}^{-2} = 1\ \text{J m}^{-3}.$$

[After Blaise Pascal (1623–62), French mathematician and philosopher, who discovered the relationship between barometric pressure and altitude.]

passage *(in biology)* the action or process of (serially) subculturing cells or microorganisms, especially with a view to adapting them to a changed environment.

passage number *(in cell culture)* the number of subcultures performed after the original isolation of the cells from a primary source.

passenger *or* **passenger DNA** any specific DNA fragment introduced into a **cloning vector** or other cloning vehicle.

passive diffusion *an alternative name for* **simple diffusion** (used especially to emphasize its distinction from **active transport**). *Compare* **facilitated diffusion**.

passive immunity immunity in an individual due to the presence of antibody or primed lymphocytes derived from another, already immune, individual.

Pasteur, Louis (1822–95), French chemist, microbiologist, and immunologist; distinguished for his pioneer work in stereochemistry (in terms of symmetry rather than molecular constitution), for his recognition of the role of microorganisms in fermentation, for his invention of the technique of heat treatment of certain fluids to prevent microbial spoilage, now known as **pasteurization**, and for devising methods of immunization against certain diseases.

Pasteur effect *or (formerly)* **Pasteur–Meyerhof effect** either the phenomenon that occurs in facultatively anaerobic cells whereby oxygen inhibits glycolysis or fermentation, or its converse whereby the rate of glycolysis or fermentation increases when oxygen is excluded. *Compare* **Crabtree effect**.

pasteurization *or* **pasteurisation** a method of heat-treating milk or similar fluids to improve storage qualities and destroy pathogenic bacteria, without markedly altering taste and nutritional characteristics. Pasteurization of milk involves heating to 65 °C for 30 minutes or to 72 °C for 15 minutes followed by rapid cooling to below 10 °C. —**pasteurize** *or* **pasteurise** *vb.*

Pasteur pipette *or* **pasteur pipette** a simple, disposable, ungraduated, dropping or transfer pipette constructed by drawing out a short length of narrow glass tubing to form a long fine tip and operated commonly by means of an attached rubber or PVC bulb or teat. Analogous devices are available moulded in low-density polyethylene, with integral bulb and sometimes calibrated. *Also (esp. US)*: **Pasteur pipet**, **pasteur pipet**.

Pasteur reaction the putative chemical reaction once considered to link fermentation and respiration and to account for the **Pasteur effect**.

patatin any of a family of glycoproteins that form 40% of the soluble protein of potato tubers. They serve as potato somatic storage proteins, and also have enzyme activity involved in host resistance. They have lipid acylhydrolase activity. Example (precursor): database code PAT0_SOLTU, 386 amino acids (42.44 kDa).

patch an intermediate stage in the formation of a **cap** (def. 2) on the surface of a cell, e.g. of a lymphocyte.

patch-clamp technique a technique whereby the conductance change of a single ion channel of an excitable membrane is measured directly. A very small electrode tip is sealed onto a patch of cell membrane, thereby making it possible to record the flow of current through individual ion channels in the patch. *See also* **Neher**, **Sakmann**.

path *see* **light path**.

+pathic *see* **+pathy**.

patho+ *or (before a vowel)* **path+** *comb. form* denoting disease or clinical disorder.

pathobiochemistry **1** the study of the biochemical processes associated with disease. **2** the processes themselves.

pathogen any agent, especially any living organism, that can cause disease.

pathogenesis the generation and production, or the origin and development, of a disease. —**pathogenetic** *adj.*

pathogenesis-related proteins proteins synthesized in plants in response to attack by fungal or bacterial pathogens. They are small proteins that belong to a limited number of families, characterized by six motifs. Example, pathogenesis-related leaf protein P14 from tomato: database code PR14_LYCE, 130 amino acids (14.24 kDa).

pathogenic (capable of) causing or producing disease. —**pathogenicity** *n.*

pathological *or* **pathologic** **1** of, or pertaining to, pathology. **2** causing, relating to, involving, or caused by disease.

pathology **1** the branch of medical science concerned with the causes and nature of disease and with the effects of disease on the structure and functioning of the organism. **2** the sum of the changes that occur in an organism as the result of a specific disease. —**pathologist** *n.*

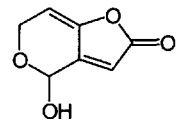
pathophysiology **1** the study of the physiological processes associated with disease. **2** the processes themselves.

pathway **1** the chain of reactions undergone by a given molecular entity or class of such entities in a particular ecosystem. **2** **metabolic pathway**.

pathway engineering the use of **genetic engineering** to change either the kinetics or the products of a metabolic pathway.

+pathy *comb. form* denoting **1** feeling, sensitivity. **2** disease of a (specified) part or kind. **3** a method of treating disease. —**pathic** *adj.*

patulin 4-hydroxy-4*H*-furo[3,2-*c*]pyran-2(6*H*)-one; a carcinogenic metabolite with antibiotic activity isolated from several fungi, particularly *Aspergillus* and *Penicillium* spp.



pauci+ *comb. form* indicating few.

paucidisperse describing a colloidal system whose dispersed phase consists of particles of only a few sizes. —**paucidispersity** *n.*

Pauli, Wolfgang (1900–58), Austrian-born US physicist; Nobel

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Laureate in Physics (1945) 'for the discovery of the Exclusion Principle, also called the Pauli Principle'.

Pauli exclusion principle *or* **exclusion principle** *or* **Pauli principle** the principle that no two electrons in an atom can be described by the same set of four quantum numbers.

Pauling, Linus Carl (1901–94), US chemist and peace campaigner; Nobel Laureate in Chemistry (1954) 'for his research into the nature of the chemical bond and its application to the elucidation of the structure of complex substances'; Nobel Laureate for Peace (1962).

Paulus filtration method a method for studying the binding of a ligand microsolute to a macrosolute. It is applicable to small amounts of material and is particularly useful for a system having a relatively low binding constant. It involves equilibration of a series of mixtures of macrosolute and ligand in a suitable solvent, then separation of unbound ligand from macrosolute-plus-bound-ligand by ultrafiltration through anisotropic membrane filters of an appropriate retentivity. The amount of microsolute retained with the macrosolute on each filter is then estimated by, e.g., radioactivity measurement or another sensitive technique. [After H. Paulus.]

Pauly's reagent a chromogenic reagent for imidazoles and phenols, consisting of a freshly prepared solution of diazotized sulfanilic acid (or other aromatic amine). In the presence of alkali, this reacts with histidine to give a red colour and with tyrosine to give an orange colour. It is useful for the identification of these amino acids on paper chromatograms.

Pavlov, Ivan Petrovich (1849–1936), Russian physiologist and experimental psychologist; Nobel Laureate in Physiology or Medicine (1904) 'for his work on the physiology of the saliva glands'. *See also* **salivary juice**.

***Pax* genes** *abbr. for* paired box genes. The **paired box** is a conserved DNA sequence that plays a role in development. *Pax* genes encode a family of transcriptional regulators specifically expressed during the development of a wide range of structures and organs, including: *Pax-1*, paraxial mesoderm derivatives; *Pax-2*, urogenital system; *Pax-3*, neural crest and pre-myoblast migration; and *Pax-6*, eye and nose.

paxillin an adhesion protein, associated with **vinculin**, that becomes phosphorylated in response to a number of stimuli, phosphorylation being associated with focal adhesion. It is also associated with dysfunction of **cadherin**-dependent cell–cell contacts and with cell spreading. Example from human: database code HSU14588, 557 amino acids (60.87 kDa).

Pb *symbol for* lead.

PBD *see* **biphenylylphenyloxadiazole**.

PBG *abbr. for* porphobilinogen.

PBI *abbr. for* protein-bound iodine.

PBP *abbr. for* pencillin-binding protein.

pBR322 a **cloning vector**.

PBS *abbr. for* phosphate-buffered saline.

PC *abbr. for* **1** paper chromatography. **2** phosphocreatine. **3** phosphatidylcholine. **4** personal computer.

pCa *symbol for* the negative logarithm of the concentration (or strictly the activity) of calcium ions in a specified solution.

PCA *abbr. for* perchloric acid.

P-cadherin placental **cadherin**.

PCB *abbr. for* pyruvate carboxylase.

PCCase *abbr. for* propionyl-CoA carboxylase.

PCMB *abbr. for* *p*-chloromercuribenzoate, or *p*-chloromercuribenzoic acid.

PCMBS *abbr. for* *p*-chloromercuribenzenesulfonate, or *p*-chloromercuribenzenesulfonic acid.

PCP *abbr. for* 1-(1-phenylcyclohexyl)piperidine (*see* **phencyclidine**).

PCR *abbr. for* polymerase chain reaction.

p.d. *abbr. for* (electric) potential difference.

Pd *symbol for* palladium.

PDB *abbr. for* protein database; a database containing 3-D protein and nucleic-acid structures. A database of the files that include the atomic coordinates is referred to as 'PDB format' or 'Brookhaven format' (after the Brookhaven National Laboratory at Upton, Long Island, New York, USA).

PDBu *abbr. for* phorbol 12,13-dibutyrate, a **phorbol ester**.

PDD *abbr. for* phorbol 12,13-didecanoate, a **phorbol ester**.

PD-ECGF *abbr. for* platelet-derived endothelial cell growth factor.

PDGF *abbr. for* platelet-derived growth factor.

pDNA *abbr. for* plasmid DNA.

P domain a domain of highly conserved cysteine residues, disulfide-bonded in the pattern 1–5, 2–4, 3–6, associated with highly conserved alanine, glycine, and tryptophan residues. Such domains are found in secretory polypeptides from animals.

Pe *symbol for* the pentyl group.

PE *abbr. for* **1** phosphatidylethanolamine. **2** potential energy.

peak **1** a sharp increase followed by a sharp decrease in a physical quantity that varies with distance, frequency, time, etc. **2** *(in chromatography)* the portion of a differential chromatogram recording the changes in detector response or eluate concentration while a given component of the applied mixture emerges from a chromatographic column. **3** the maximum value of a **peak** (def. 1, 2).

pEC_{50} *see* **$p[A]_{50}$**.

PEC-60 a 60-amino-acid endogenous regulatory polypeptide abundant in intestinal tissue and also found in the central nervous system. It inhibits the formation of cyclic AMP and activates Na^+,K^+-ATPase. It is structurally related to pancreatic secretory trypsin inhibitor and inhibits insulin secretion. Example from *Sus scrofa* (precursor): database code PE60_PIG, 86 amino acids (9.63 kDa).

PECAM *abbr. for* platelet endothelial cell adhesion molecule; a class of **adhesion molecules** represented by PECAM-1 (*or* CD31), a member of the immunoglobulin superfamily. It is constitutively expressed on endothelial cells, platelets, granulocytes, monocytes, and T cells, and participates in homophilic binding (i.e. binding to itself). It is required for transmigration of leukocytes across the endothelium during extravasation. Example from human (precursor): database code PEC1_HUMAN, 738 amino acids (82.54 kDa), residues 1–27, signal; 28–738, PECAM.

pectate any salt or ester of **pectic acid**.

pectic acid the form of **pectin** (def. 1) that is essentially free of methyl ester groups.

pectic substance *an alternative name for* **pectin** (def. 1).

pectin **1** *or* **pectic substance** any mixture of complex, colloidal, macromolecular plant **galacturonans** containing a large proportion of D-galactopyranosyluronic acid residues in ($\alpha 1 \rightarrow 4$) linkage, the carboxyl groups of which may be esterified to varying degrees by methyl groups or be partially or completely converted to salts; some D-arabinose and D-galactose residues nearly always occur in addition, and residues of certain other sugars are sometimes present. M_r is usually in the range 1×10^4–4×10^5. Pectins are important matrix polysaccharides of plant cell walls, especially those of higher plants, sometimes constituting as much as one-third of the dry matter; they also occur in some plant juices. Certain fruits are particularly rich in pectin. **2** *(in commerce)* a whitish, water-soluble powder prepared from the rind of citrus fruits or apple **pomace** by extraction with dilute acid and consisting essentially of **pectin** (def. 1). It is used *inter alia* in the preparation of jams because of its ability to form gels in the presence of sucrose at high concentrations.

pectinase *see* **polygalacturonase**.

pectinesterase EC 3.1.1.11; *other names*: pectin methylesterase, pectin methoxylase; an enzyme that hydrolyses pectin to methanol and **pectic acid**. It is found in plant cell walls. One role may be concerned with cell-wall metabolism during fruit ripening. Example from *Lycopersicon esculentum* (tomato): PME1_LYCES, 317 amino acids (34.55 kDa).

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pectinic acid the form of **pectin** (def. 1) in which a high proportion of the carboxyl groups are esterified with methanol.

pectin lyase EC 4.2.2.10; an enzyme that catalyses a *trans* elimination to convert pectin to oligosaccharides with unsaturated (C-4,C-5) terminal residues. Although often described as 4-deoxy-6-methyl-α-D-galact-4-enuronosyl groups, they are more accurately termed 4-deoxy-6-methyl-β-L-*threo*-hex-4-enopyranouronosyl groups. Example (precursor) from *Aspergillus niger*: database code PLYA_ASPNG, 379 amino acids (39.85 kDa).

pectin sugar *an old name for* L-arabinose.

PEG *abbr. for* polyethylene glycol.

PEI *abbr. for* the poly(ethyleneimine) group,

pelargonate *another name for* **nonanoate**.

pelargonoyl *another name for* **nonanoyl**.

pellagra a disease of animals, including humans, arising from a dietary deficiency of **nicotinic acid**, especially in the absence of sufficient dietary tryptophan to generate adequate amounts of nicotinamide coenzymes metabolically. This situation can occur when the diet consists largely of maize (corn). Pellagra is characterized by scaly dermatitis on exposed skin surfaces, diarrhoea, and depression.

pellagra-preventative factor *abbr.*: PP factor *or* PPF; *a former name for* **nicotinic acid** or nicotinamide.

pellet a small compressed mass of material, especially such a mass deposited at the bottom of a tube by centrifugation of a suspension.

pellicle a thin skin, membrane, or film.

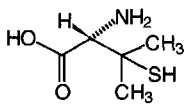
pellicular **1** of, relating to, or being in the form of a pellicle. **2** describing a type of column packing, used in high-pressure liquid chromatography, in which the stationary phase is present as a thin layer on the surface of tiny glass beads.

Peltier effect the phenomenon whereby heat is given out, or absorbed, when an electric current passes across a junction between two dissimilar materials. *See* **thermocouple**. *Compare* **Seebeck effect**. [After Jean Peltier (1785–1845), French physicist.]

penatin *an obsolete name for* **glucose oxidase**.

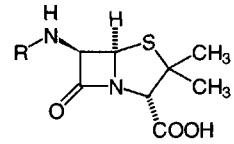
penetrance *(in genetics)* the degree to which a particular genotype is expressed in a population phenotype. If every individual carrying a dominant mutant gene shows the mutant phenotype, the gene is said to show complete penetrance.

penicillamine 3-mercapto-D-valine; β,β-dimethylcysteine; 2-amino-3-methyl-3-mercaptobutyric acid; the D-enantiomer is a characteristic degradation product of penicillin-type antibiotics. It is a potent chelator of heavy metal ions, hence it is used clinically in the treatment of **Wilson's disease** and of poisoning by metals such as copper, lead, and mercury.



penicillic acid 3-methoxy-5-methyl-4-oxo-2,5-hexadienoic acid (exists in equilibrium with lactone form); a toxic antibiotic metabolite obtained from several fungi. It bears no relationship to penicillin or its degradation products. (Illustrated opposite.)

penicillin **1** *the generic name for* a range of related antibiotics, whether produced naturally during the growth of various microfungi of the genera *Penicillium* and *Aspergillus* or of semisynthetic origin, that contain the condensed β-lactam–thiazolidine ring system:

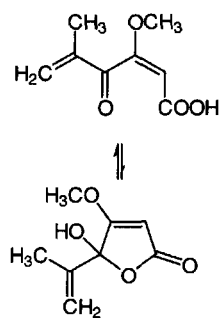


where R is any one of a variety of acyl groups such as: phenylacetyl, C_6H_5–CH_2–CO– (in **penicillin G**, **penicillin II**, **benzylpenicillin**); phenoxyacetyl, C_6H_5–O–CH_2–CO– (in **penicillin V**); and D-adipyl, HOOC–$CH(NH_2)$–$[CH_2]_3$–CO– (in **penicillin N**, *also called* **cephalosporin N**). Only those enantiomers having the D-configuration at C-2 of the thiazolidine ring show antibiotic activity. The parent substance, **6-aminopenicillanic acid**, in which R is H, has little intrinsic antibiotic activity but is important as the naturally occurring starting point for the semisynthesis of artificial penicillins, e.g. **ampicillin**, in which R is aminophenylacetyl, C_6H_5–$CH(NH_2)$–CO– . All penicillins are readily inactivated by chemical or enzymic hydrolysis of the strained four-membered β-lactam ring, cold dilute acid yielding **penicillamine**, and alkali or penicillinases and other β-lactamases forming the corresponding substituted **penicilloic acids**. The penicillins generally have extremely low toxicity to animals and a high antibacterial activity, especially against Gram-positive organisms, the spectrum of activity varying somewhat with the nature of the group R. They act by inhibiting cross-linking of peptidoglycan in the cell wall of growing bacterial cells, the consequent structural weakness of the wall rendering the cells sensitive to osmotic lysis. **2** the (hypothetical) substance 6-formamidopenicillanic acid, used only in combination in trivial names of certain **penicillins** (def. 1), e.g. benzylpenicillin.

penicillin acylase EC 3.5.1.11; *recommended name*: penicillin amidase; an enzyme that catalyses the hydrolysis of penicillin to a fatty-acid anion and 6-aminopenicillinate. There are several enzymes that differ in specificity for the fatty acid. Examples: **penicillin V acylase** (*or* penicillin V amidase), a homotetramer from *Bacillus sphaericus*, database code PAC_BACSH, 338 amino acids (37.42 kDa); **penicillin G acylase** (*or* penicillin G amidohydrolase) from *Escherichia coli*, database code PAC_ECOLI, 846 amino acids (94.54 kDa) – the latter sequence represents a zymogen for a periplasmic enzyme comprising a signal (amino acids 1–26), an α subunit (27–235), a spacer (236–289) and a β subunit (290–846); the active enzyme is a heterodimer (α,β). *See also* **6-amino-penicillanic acid**.

penicillin amidase *the recommended name for* **penicillin acylase**.

penicillinase *a trivial name for* any **β-lactamase** that acts preferentially on penicillins.



penicillic acid

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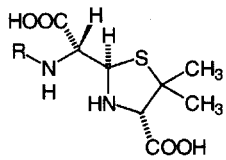
penicillin-binding protein *abbr.*: PBP; any of various bacterial proteins that are capable of binding penicillin(s) covalently. Such proteins appear to be located predominantly, if not solely, in the cytoplasmic membrane of all species of bacteria in which peptidoglycan occurs in the cell wall. These proteins are believed to catalyse reactions in the later stages of cell-wall synthesis and there is a strong presumption that at least one of them catalyses the insertion of nascent peptidoglycan into the cell wall. In Gram-negative bacteria some penicillin-binding proteins are known to be involved in the maintenance of cell shape or in cell elongation or septation. Another is a carboxypeptidase, example from *Haemophilus influenzae* (precursor): database code DACA_HAEIN, 393 amino acids (43.41 kDa).

penicillin G acylase *see* **penicillin acylase**.

penicillin V acylase *see* **penicillin acylase**.

penicilloic acid any of a range of compounds of structure:



and produced by cleavage of the β-lactam ring of **penicillins** (def. 1) by enzymic or alkaline hydrolysis.

penta+ *or (before a vowel)* **pent+** *comb. form* denoting five, fivefold, five times.

pentacosa+ *comb. form* denoting 25, 25-fold, 25 times.

pentadeca+ *comb. form* denoting 15, 15-fold, 15 times.

pentafunctional arom polypeptide a polypeptide that catalyses five consecutive enzymatic reactions in prechorismate polyaromatic amino-acid biosynthesis, i.e the second to sixth steps in the biosynthesis from chorismate of the aromatic amino acids (the **shikimate pathway**). It occurs in some yeasts and other fungi and in *Euglena gracilis*. It contains: **3-dehydroquinate synthase**, **3-dehydroquinate dehydratase**, **shikimate 5-dehydrogenase**, **shikimate kinase**, and **EPSP synthase**. Example from yeast: database code AROI_ YEAST, 1588 amino acids (174.55 kDa). Residues 1–392 = 3-dehydroquinate synthase; residues 404–866 = EPSP synthase; residues 887–1060 = shikimate kinase; residues 1061–1293 = 3-dehydroquinate dehydrogenase; and residues 1306–1588 = shikimate dehydrogenase.

pentagastrin *the trivial name for* (*N-tert*-butyloxycarbonyl-β-alanyl)-L-tryptophanyl-L-methionyl-L-aspartyl-L-phenylalaninamide; a synthetic analogue of **gastrin** that consists of the latter's C-terminal tetrapeptide amide sequence with an added protected N-terminal β-alanyl residue. It is used in the **pentagastrin test** as a gastrin analogue to stimulate gastric-acid secretion, which is then measured. Secretion is sometimes high in patients with duodenal ulceration and low in patients with gastric ulcer, but this is too variable to be of great use in diagnosis. *See also* **calcitonin**.

pentamer **1** any oligomer consisting of or derived from five monomers. **2** the group of five capsomeres in an icosahedral virus capsid.

pentanoate *another name for* **valerate**.

pentanoyl *another name for* **valeryl**.

pentaose a pentasaccharide in which all the residues are of one type and uniform linkage. *Compare* **pentose**.

pentaric acid any **aldaric acid** obtained by oxidation of a **pentose** at C-1 and C-5.

pentasaccharide any oligosaccharide composed of five monosaccharide units. Pentasaccharides occur in small amounts in plants, e.g. **verbascose** in soybeans.

pentaxin *or* **pentraxin** any of a family of proteins with a discoid appearance under electron microscopy, having five non-covalently bound subunits. The family includes **C-reactive protein**, serum amyloid P-component, and neuronal pentaxins. Example from human, neuronal pentaxin II (precursor): database code NPX2_HUMAN, 430 amino acids (46.81 kDa); residues 1–15 are the signal, 16–430 neuronal pentraxin II; residues 226–430 contain the pentaxin domain.

pentitol any **alditol** having a chain of five carbon atoms in the molecule.

pentobarbital 5-ethyl-5-(1-methylbutyl)barbiturate; a major barbiturate drug. *One proprietary name* is Nembutal.

pentolinium test a test in which **pentolinium**, a sympathetic ganglion blocking drug, is used to reduce catecholamine secretion; failure to achieve reduction may indicate a **pheochromocytoma**.

penton a capsomere that is surrounded by five other capsomeres in an icosahedral virus capsid.

pentonic acid any monocarboxylic acid (aldonic acid) formally derived from a pentose by oxidation at C-1.

pentosan a **glycan** that yields only pentoses on hydrolysis.

pentose any **aldose** having a chain of five carbon atoms in the molecule. *Compare* **pentaose**.

pentose cycle *an alternative name for* **pentose phosphate pathway**.

pentose nucleic acid *abbr.*: PNA; *a former term for* **ribonucleic acid**.

pentose phosphate pathway *or* **hexose monophosphate pathway** a complex series of extramitochondrial metabolic reactions by which glucose 6-phosphate is oxidized with formation of carbon dioxide, ribulose 5-phosphate, and reduced NADP, the ribulose 5-phosphate then entering a series of reactions in which a number of sugar phosphates containing between three and seven (or eight) carbon atoms are successively interconverted. One consequence of these interconversions is the nonoxidative regeneration of glucose 6-phosphate, which then can enter the pathway for another cycle of oxidative decarboxylation and skeletal rearrangement, the eventual result being the complete oxidation of one molecule of glucose with the formation of six molecules of carbon dioxide and 12 molecules of NADPH. The pathway thus provides (in some organisms or tissues) an alternative route to (or shunt of) part of the glycolytic pathway; it also provides ribose 5-phosphate for nucleotide synthesis and (in some organisms) other intermediates for biosynthesis. Of special importance is D-erythrose 4-phosphate, required for the biosynthesis of aromatic amino acids and many other materials by the **shikimate** pathway. In higher plants many of the enzymes of the pathway function in the reverse direction as part of the **reductive pentose phosphate cycle**. *Other names*: hexose monophosphate shunt; pentose cycle; phosphogluconate (oxidative) pathway; Warburg–Dickens pathway; Warburg–Dickens–Horecker pathway. *See also* **glucose-6-phosphate dehydrogenase**, **phosphogluconate**, **phosphogluconate dehydrogenase (decarboxylating)**, **transaldolase**, **transketolase**.

pentosuria the presence of excessive amounts of pentose in the urine. Two types may be distinguished: (1) **essential pentosuria**, in which daily excretion of 1–4 g L-xylulose (normal <60 mg) occurs due to an inherited diminished activity of the NADP-linked L-xylulose reductase (EC 1.1.1.10), an enzyme of the glucuronate pathway that converts L-xylulose to xylitol; (2) **alimentary pentosuria**, in which excretion of up to 100 mg of L-arabinose or L-xylose occurs following ingestion of unusually large amounts of such fruits as cherries, grapes, and plums.

pentraxin *see* **pentaxin**.

pentulose any **ketose** having a chain of five carbon atoms in the molecule. There are two enantiomeric pairs of pentuloses having the carbonyl group at C-2, these being the D- and L-isomers of ribulose, *erythro*-2-pentulose, and of xylulose, *threo*-2-pentulose.

pentyl *symbol*: Pe; the alkyl group, CH_3–$[CH_2]_3$–CH_2–, derived from pentane.

PEP *abbr. for* phospho*enol*pyruvate.

PEPCK *abbr. for* phospho*enol*pyruvate carboxykinase.

peplomer a virus-coded proteinaceous knob or spike, numbers

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of which project from the peplos (i.e. **envelope** (def. 3)) of an enveloped virus particle. Peplomers may have cell-receptor, hemagglutinating, or neuramidinase activity.

peplos *an alternative name for* **envelope** (def. 3).

pepsin **1** any of a small family of closely related aspartic proteinase enzymes of 31–36 kDa that together give rise to the principal proteinase activity of gastric juice of vertebrates. The family includes **pepsin A**, **pepsin B**, pepsin C (i.e. **gastricsin**), and **pepsin D**. Pepsins have maximal activity at pH values in the range 2–3; they preferentially catalyse hydrolysis of peptide bonds formed from hydrophobic amino-acid residues, the detailed specificity varying somewhat between the different pepsins. **2** *an alternative name for* **pepsin A**.

pepsin A *or* **pepsin** *abbr. (in clinical chemistry)*: PPS; *the recommended name for* the predominant enzyme (EC 3.4.23.1) of the **pepsin** family. It is a single-chain phosphoprotein of (in the pig) 327 amino-acid residues, formed by limited proteolysis of pepsinogen A. It preferentially cleaves peptide bonds where the residues on either side are formed from hydrophobic amino acids; for example, in the B chain of insulin it cleaves Phe^{1}-|-Val^{2}, Gln^{4}-|-His^{5}, Glu^{13}-|-Ala^{14}, Ala^{14}-|-Leu^{15}, Leu^{15}-|-Tyr^{16}, Tyr^{16}-|-Leu^{17}, Gly^{23}-|-Phe^{24}, Phe^{24}-|-Phe^{25}, and Phe^{25}-|-Tyr^{26} bonds (*compare* **pepsin B**). The unphosphorylated form of porcine pepsin A is called pepsin D.

pepsin B *or* **parapepsin I** a pig enzyme (EC 3.4.23.2) of the **pepsin** family. It is a single-chain phosphoprotein of 332 amino-acid residues, formed by limited proteolysis of pig pepsinogen B. It has little activity towards hemoglobin as substrate (*compare* **gastricsin**), but degrades gelatin. Its specificity on the B chain of insulin is more restricted than **pepsin A**; it does not cleave Phe^{1}-|-Val^{2}, Gln^{4}-|-His^{5}, or Gly^{23}-|-Phe^{24}.

pepsin C *an alternative name for* **gastricsin**.

pepsin D unphosphorylated pig **pepsin A**.

pepsinogen a precursor (i.e. zymogen) of a **pepsin** enzyme; pepsinogens A, B, and C give rise to **pepsin A**, **pepsin B**, and pepsin C (i.e. **gastricsin**) respectively. Pepsinogens are secreted by the chief cells of the gastric mucosa of vertebrates. In pepsinogen, the active site is conformationally masked at neutral pH, and exposed as the pH falls after secretion into the stomach. The first bond breakage causes the release of residues 1–16, leaving a peptide known as **pseudopepsin**. Thereafter, a further 28 residues are removed in stages to form the active enzyme. Pepsinogen C is also secreted by the mucosa of the proximal duodenum. Example from human: database code PEPA_HUMAN, 388 amino acids (41.93 kDa): this is the pepsinogen precursor with a signal peptide; pepsin is from residue 63 to the end.

pepstatin A *N*-isovaleryl-L-valyl-L-valyl-3-hydroxy-6-methyl-4-aminoheptanoyl-L-alanyl-3-hydroxy-6-methyl-4-aminoheptanoic acid; a peptide, isolated from broth cultures of *Streptomyces* spp., that inhibits pepsin and other aspartic proteinases, notably cathepsin D, renin, and fungal acid proteinases.

peptaibophol *or* **peptaibol** any of a group of peptide amide antibiotics, 15–24 residues long and containing up to 40% α-aminoisobutyric acid residues. The members of this group, emerimicin, zervamicin IIA, antiamoebin I, sizukacillin A, and **alamethicin**, are all capable of altering the permeability of phospholipid bilayers. The N termini are acylated and the C-terminal carboxyl groups are in amide linkage with phenylalaninol.

peptic **1** of, pertaining to, caused by, or containing **pepsin**. **2** of, pertaining to, or promoting digestion.

peptidase *or* **peptide hydrolase** *or* **protease** any enzyme that hydrolyses peptide bonds. The group includes the **exopeptidases**, such as the aminopeptidases and carboxypeptidases, (sub-subclasses EC 3.4.11–19) and the **endopeptidases** (sub-subclasses EC 3.4.21–99). The 1992 revision of *Enzyme Nomenclature* (published for IUBMB by Academic Press) should be consulted for more detail.

peptidase P-sites sites adjacent to or near the cleaved site in peptidase substrates; in describing the specificity of peptidases, it is useful to have a convention for identifying the residues on either side of the cleaved bond; the following model is often followed (the cleaved, or scissile bond is indicated as -|-, and the N terminus is as usual to the left):

-P3-P2-P1-|-P1′-P2′-P3′-.

Compare **peptidyl site**.

peptide any compound containing two or more amino-acid residues joined by amide bond(s) (*see* **peptide bond**) formed from the carboxyl group of one amino acid (residue) and the amino group of the next one. The term peptide usually applies to compounds in which the amide bond(s) are formed between C-1 of one α-amino acid (residue) and N-2 of another, but it includes compounds in which the residues are linked by other amide bonds. *See also* **oligopeptide**, **polypeptide**. —**peptidic** *adj.*

peptide antibiotic any member of a diverse group of antibiotics containing amino-acid residues, some of which are often of the D-form, linked to one another by peptide bonds, to hydroxy acids by depsipeptide bonds, and frequently also to additional components; the structure is often cyclic. The group includes the **bacitracins**, **gramicidins**, **polymyxins**, and **tyrocidins**.

peptide bond *or* **peptide linkage** any amide bond formed between two amino acids (or amino-acid residues). The term usually denotes the amide bond (sometimes called the **eupeptide bond**) formed between an α-amino group of one amino acid and an α-carboxyl group of another amino acid, but it also includes any amide bond (sometimes called an **isopeptide bond**) formed from an amino group and a carboxyl group either or both of which are in other positions in the contributing amino acids.

peptide chain *or* **polypeptide chain** any discrete linear sequence of amino-acid residues linked by eupeptide bonds, especially in a larger molecular structure. *See* **peptide bond**.

peptide HI *abbr.*: PHI; a 27-residue peptide amide, also known as PHI-27, found in intestinal tissue, brain, respiratory tract, and pancreas. It stimulates insulin secretion and pancreatic exocrine secretion, causes vasodilation, increases intestinal fluid transport, relaxes smooth muscle, and is a potent prolactin-releasing factor. It shows sequence homology with gastric inhibitory polypeptide, glucagon, secretin, and vasoactive intestinal polypeptide; human PHI has the sequence

HADGVFTSDFSKLLGQLSAKKYLESLM-NH_2

(porcine PHI has Arg^{12} and Ile^{27}; bovine has Tyr^{10}, Arg^{12}, and Ile^{27}). It is named after the single-letter codes, H and I, for the histidine and isoleucine residues at the N and C termini respectively of the porcine and bovine peptides.

peptide histidine valine 42 *abbr.*: PHV 42; a peptide with N-terminal histidine and C-terminal valine, having 42 residues derived from residues 81–122 of prepro-vasoactive intestinal peptide.

peptide hormone *or* **polypeptide hormone** any peptide with hormonal activity in animals, whether endocrine, neuroendocrine, or paracrine. Such substances form a very diverse group physiologically, and the boundary between peptide hormones and protein hormones is somewhat indistinct.

peptide hydrolase *another name for* **peptidase**.

peptide linkage **1** *an alternative name for* **peptide bond**. **2** chemical linkage between structural components of a molecule by means of peptide bonds.

peptide map a pattern, characteristic of a particular polypeptide or protein, produced by partial hydrolysis followed by two-dimensional fractionation of the resultant peptides (and amino acids) by chromatography and/or electrophoresis.

peptide nucleic acid a synthetic DNA analogue with an *N*-(2-aminoethyl)glycine backbone that mimics DNA in forming a **heteroduplex**.

peptidergic **1** describing any nerve that is activated by a peptide agonist. **2** describing any nerve that acts by releasing a

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peptide agonist from its nerve endings, whether into a synapse with another neuron, into intercellular fluid, or directly into the bloodstream.

peptide synthesis **1** *(in biology) see* **protein and peptide biosynthesis**. **2** *(in chemistry)* the synthesis, by chemical means, of peptides. A number of strategies are possible, including automated methods. The first step is the protection, in the amino-acid reactants, of reactive groups not involved in peptide bond formation (*see* **protecting groups**); peptide-bond formation is then achieved by activation of the carboxyl group, which is reacted with the free α-amino group of another amino acid. A variety of methods have been used for activation of the carboxyl group but a frequently used method is to react it with *N*-hydroxysuccinimide or a derivative to form an acyl succinimido ester, which reacts under mild conditions with free amino groups. Normally, and always in automated methods, the carboxyl group of the first amino acid is attached to a resin, by a bond that is easily detached later, so that the desired product, the growing peptide chain, remains attached to the resin which facilitates its purification; this technique, called **solid-phase peptide synthesis**, was pioneered by **Merrifield**.

peptide unit *(in crystallography)* any sequence of atoms in a peptide chain that may be represented by the general formula –CHR–CO–NH–, where R denotes the side chain of an amino-acid residue. *Compare* **amino-acid residue**.

peptide YY *abbr.*: PYY; a 36-residue peptide amide originally found in porcine upper small intestinal tissue. It is a gut hormone that inhibits exocrine pancreatic secretion. Members of this family regulate numerous physiological processes, including appetite, gastrointestinal transit, anxiety, and blood pressure. It shows sequence homology with **neurotensin** and **pancreatic hormone**, having the amino-acid sequence:

YPIKPEAPGEDASPEELNRYYASLRHYLNLVTR-QRYNH$_2$.

It is named after the single-letter code, Y, for the tyrosine residues at its N terminus and the tyrosine amide at its C terminus.

peptido+ *comb. form* indicating the presence of peptide linked to some other (specified) component(s).

peptidoglycan *or* **murein** any of a class of glycoconjugates found only in bacterial cell walls and consisting of strands of glycosaminoglycan cross-linked by oligopeptides to form a huge and rigid network. There are characteristic differences between peptidoglycans of eubacteria and those of archaebacteria. The glycosaminoglycan strands are formed of alternating residues, usually *N*-acetylated or *N*-glycoloylated, of D-glucosamine and either muramic acid (in Bacteria) or L-talosaminouronic acid (in Archaea); the carboxyl groups of the muramic-acid residues are commonly joined in amide linkage to oligopeptides containing residues of both L- and D-amino acids whereas those of the L-talosaminouronic-acid residues are linked to peptides consisting of L-amino acids only. The peptide side-chains of adjacent polysaccharide strands are sometimes crosslinked between a carboxyl group of one peptide moiety and an amino group of another, either directly by a peptide bond or indirectly by an interpeptide bridge consisting of one to several amino-acid residues.

peptidyl the acyl group formed from a peptide by removal of the hydroxyl group from its C-terminal carboxyl group.

peptidylprolyl isomerase *abbr.*: PPIase; EC 5.2.1.8; *systematic name*: peptidylproline *cis–trans*-isomerase; an enzyme that irreversibly converts prolyl residues within a polypeptide chain from a *trans* to a *cis* configuration; the reaction is:

peptidylproline (ω = 180) = peptidylproline (ω = 0).

It accelerates protein folding. There are at least two families of enzymes with this activity. One is identical to **cyclophilin**, an **immunophilin** that is the major high-affinity binding protein of the immunosuppresive drug **cyclosporin A**. Another class of immunophilins that exhibit isomerase activity are the FK506-binding proteins (*see* **FKBP**). The physiological role of these proteins is unresolved. The peptide Ala-Pro inhibits the reaction but is not a substrate. Example from human: database code FKB3_HUMAN, 141 amino acids (15.64 kDa).

peptidyl site *or* **P-site** *or (more correctly)* **peptidyl-tRNA site** the ribosomal site to which a newly elongated peptidyl-tRNA molecule is transferred from the aminoacyl site during the sequence of polypeptide biosynthesis reactions, and at which it displaces the tRNA molecule remaining from the previous elongation step. *Compare* **peptidase P-site**. *See also* **ribosome**.

peptidyltransferase EC 2.3.2.12; the ribosomal enzyme that catalyses the elongation step in polypeptide synthesis:

peptidyl-tRNA$_1$ + aminoacyl-tRNA$_2$ = tRNA$_1$ + peptidyl-aminoacyl-tRNA$_2$.

It is an activity of the large ribosomal subunit involving, in bacteria, **ribosomal proteins** L2, L3, L4, L15, and L16, and 23S rRNA. *See also* **peptidyl site**.

peptidyl-tRNA the form in which a growing polypeptide chain is held to a ribosome during polypeptide biosynthesis. The polypeptide is esterified through its C-terminal carboxyl group to the 3′-hydroxyl of the adenosine residue at the 3′ end of a molecule of tRNA. *See* **protein synthesis**.

peptize *or* **peptise** to disperse (an aggregate) to form a colloidally stable suspension or emulsion; especially to convert (a gel) into a sol. —**peptization** *or* **peptisation** *n.*

peptolide *(sometimes)* any naturally occurring cyclodepsipeptide; *see* **depsipeptide**.

peptone any soluble mixture of products, 0.6–3 kDa, of the partial enzymic (or acid) hydrolysis of proteinaceous material. It is used as a constituent of many microbiological culture media.

peptonize *or* **peptonise** **1** to convert (proteinaceous material) into **peptone**. **2** to combine with peptone; e.g. peptonized iron.—**peptonization** *or* **peptonisation** *n.*

per+ *comb. form* denoting **1** through, throughout, beyond; e.g. perennial. **2** *(in chemistry)* **a** (of an indicated element) being in a higher than usual state of oxidation; e.g. periodate. *See also* **peracid** (def. 1). **b** containing a higher than normal proportion of (an indicated element); e.g. **peroxide**. *See also* **peroxoacid**, **peroxy acid**. **c** (in the trivial names performic, peracetic, and perbenzoic acids) **peroxy+**. **d** exhaustive replacement of hydrogen (except any in a characteristic group) in an organic compound by (an indicated halogen); e.g. perfluoropentane, C_5F_{12}. *See also* **perhydro**.

peracid *or* **per-acid** **1** *a common name for* any inorganic acid in which the central element of the acid is in its highest state of oxidation. **2** *a common name for* **peroxoacid**. **3** *a common name for* **peroxy acid**.

per cent *or* **percent** *symbol*: %; containing or consisting of a specified numerical proportion (of some component in relation to a whole) expressed as a number fraction multiplied by 100; bearing a specified numerical relationship (to some quantity) similarly expressed. When the term per cent or the symbol % is applied to a solution, one of the designations w/w, w/v, or v/v may be appended according as the units used are mass per mass, mass per volume, or volume per volume, respectively.

percentage proportionality expressed per cent; it is used especially to qualify a substantive, e.g. percentage error.

perchloric acid *abbr.*: PCA; chloric(VII) acid, $HClO_4$; a compound used in chemical analysis as an oxidizing agent.

Percoll *the proprietary name for* a polydisperse preparation of colloidal silica particles rendered nontoxic to cells by a coating of polyvinylpyrollidone. Aqueous dispersions of the material can be used to generate density gradients for the separation of cells, viruses, or cell organelles by sedimentation.

percutaneous through the skin; used especially of the route of administration of drugs applied to the skin.

perforin a lymphocyte pore-forming protein; it is produced by cytotoxic T cells when these are in contact with target cells,

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being stored in secretory vesicles and released by local exocytosis. With Ca^{2+}, it polymerizes into transmembrane tubules that form pores in the target-cell membrane and is thus capable of lysing nonspecifically a variety of target cells. Example (precursor) from human: database code PERF_HUMAN, 555 amino acids (61.31 kDa).

performic acid *the trivial name for* peroxyformic acid, H–C(=O)–O–OH; a strong oxidizing agent, useful in protein chemistry for cleavage of any disulfide bond, R–S–S–R′, to the corresponding pair of sulfonic acid groups, $R–SO_3H$ + $R′–SO_3H$, e.g. of a cystine residue to two cysteic-acid residues. Tryptophan residues are also oxidized, and methionine residues are converted to methionine *S*,*S*-dioxide residues.

perfusate any fluid used for a perfusion.

perfuse to pass fluid through an organ or tissue, especially artificially. —**perfusion** *n.*

perhydro+ *prefix (in chemical nomenclature)* signifying conversion of the indicated unsaturated organic compound to the corresponding fully hydrogenated compound; used especially where the parent compound is markedly unsaturated; e.g. perhydroanthracene, $C_{14}H_{24}$ (formed from anthracene, $C_{14}H_{10}$).

peri+ *comb. form* enclosing, surrounding; near.

pericellular surrounding a cell or cells.

perifusate any fluid used for a perifusion (*see* **perifuse**).

perifuse to pass a fluid around isolated cells or cell clusters in suspension. —**perifusion** *n.*

***peri*-fused** *see* ***ortho*- and *peri*-fused**.

perikaryon *or* **cell body** the cytoplasm immediately surrounding the nucleus of a neuron.

perilipin a protein found in adipocytes exclusively at the surface of the lipid storage droplets that serves as the major A-kinase substrate. It is a major hormonally regulated adipocyte-specific phosphoprotein. Example, perilipin A from *Rattus norvegicus*: database code A49413, 517 amino acids (55.55 kDa).

perinuclear space the zone, 20–40 nm wide, between the two lipid bilayers of the **nuclear envelope** of a eukaryotic cell.

period **1** a specified or defined length of time, especially the time occupied by one complete cycle of some regularly recurring phenomenon or event. **2** *(in chemistry)* any of the horizontal rows of chemical elements in the **periodic table**.

periodate **1** any anion derived from a **periodic acid**, especially the anion, IO_4, derived from metaperiodic acid. **2** any salt of a periodic acid, especially of metaperiodic acid or orthoperiodic acid.

periodate oxidation a method for the investigation of the structure of organic molecules, based upon the ability of aqueous periodate (or periodic acid) to cleave specifically and quantitatively any carbon–carbon single bond where one carbon atom carries a hydroxyl group and the other carries an amino, carbonyl, carboxyl, or hydroxyl group, these groups being oxidized and the periodate reduced to iodate. The method is particularly useful in the structural analysis of carbohydrates. *See also* **periodic acid–Schiff reaction**.

periodic **1** of, relating to, or resembling a **period** (def. 1 or 2); happening or occurring in periods; intermittent; cyclical. —**periodically** *adv.* **2** *(in chemistry)* denoting any of several oxoacids of iodine containing a greater proportion of oxygen than iodic acid. *See* **per+** (def. 2a), **periodic acid**.

periodic acid any of a number of iodic(VII) acids formed by the combination of iodine heptoxide, I_2O_7, with water in different molecular proportions, especially **orthoperiodic acid** (formerly known as paraperiodic acid), H_5IO_6; **metaperiodic acid**, HIO_4, exists mainly as its salts. These acids and their salts are strong oxidizing agents.

periodic acid–Schiff reaction *abbr.*: PAS reaction; a chromogenic reaction used as a sensitive test for carbohydrate, either histochemically or in chromatography. It is based on the periodate oxidation of *vicinal* –CHOH– groups to –CHO groups and the subsequent reaction of these with **Schiff reagent** to give a characteristic magenta colour.

periodic classification *see* **periodic system**.

periodicity the recurrence (of some phenomenon or event) at constant intervals in space or time; a measure of the frequency of such recurrence.

periodic law *or* **Mendeleev's law** the principle that the properties of the chemical elements are a periodic function of their atomic numbers (originally, of their atomic weights).

periodic system *or* **periodic classification** any classification of the chemical elements on the basis of the **periodic law**.

periodic table a mode of representing the **periodic system**; it is a tabular arrangement of the chemical elements in horizontal rows and vertical columns in order of increasing proton number row by row, each row, or **period**, consisting of those elements from an alkali metal to the rare gas of next highest proton number (except for the last, incomplete, period) and each column, or **group**, consisting of a family or set of those elements with similar chemical properties. Over the years, numerous versions of such a tabular arrangement have been proposed and used, the three commonest formats having 8, 18, or 32 columns of elements. Of these, the ones most widely adopted latterly have been variations of the so-called long periodic table, in which there are 18 columns. The particular version of the long table illustrated on the endpapers is the one currently recommended by IUPAC and adopted for use elsewhere in this dictionary. In this IUPAC periodic table, as similarly in other versions of the long table, the 15 elements of proton numbers 57 to 71, the **lanthanoids**, occupy a single position in period 6 of group 3, and those of numbers 89 to 103, the **actinoids**, a single position in period 7 of group 3, practical considerations requiring these elements to be listed separately at the bottom of the table.

In previous versions of the long table it was usual for 14 of the columns to be formed into seven groups, numbered I to VII and each divided into A and B subgroups. However, these subgroup designations were not always applied the same way round, with the consequence that two alternative conventions for the long table have concurrently had widespread support – one commonly in Europe (and hitherto followed in principle by IUPAC), the other in North America and elsewhere. Furthermore, the three columns containing the elements iron, cobalt, and nickel, originally designated together as group VIII, and the eighteenth column, containing the noble gases and originally designated as group O, have sometimes been labelled group VIIIA and group VIIIB respectively in the European version of the table, whereas in the North-American version the noble gases have in recent years been assigned usually to group VIIIA. The resultant confusion led IUPAC to recommend in 1990 that the columns of the long periodic table now be serially numbered as groups 1 to 18. The correspondence of the group designations in the new IUPAC periodic table with those of the European and North-American conventions in recent use is also shown in the endpapers.

peripheral (cell-membrane) protein *or* **extrinsic protein** *an operational term for* any protein that can be dissociated unchanged from a cell membrane by a mild treatment such as increase in ionic strength of the medium or addition of a chelating agent to it. Such proteins are presumed to be loosely attached to one or other surface of the cell membrane. *Compare* **integral (cell-membrane) protein**.

peripheral nervous system the part of an animal's nervous system other than the **central nervous system**, and generally located in the peripheral, or outer, parts of the body. It comprises the cranial nerves and spinal nerves and their branches, and includes the **autonomic nervous system**. It serves to link effector organs and sensory receptors with the central nervous system.

peripherin a glycoprotein, named from 'peripheral vision', that is essential for eye-disk morphogenesis; it is probably an adhesion molecule. Example from human: database code RDS_HUMAN, 346 amino acids (39.14 kDa).

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periplasm *or* **periplasmic space** the region in a bacterial cell between the cell membrane and the cell wall.

peristalsis a wavelike sequence of involuntary muscular contraction and relaxation that passes along a tubelike structure, such as the intestine, impelling the contents onwards. —**peristaltic** *adj.*

peristaltic pump a pump that functions, by analogy with the action of **peristalsis**, by the repeated compression of a length of elastic tubing in such a way as to cause the contents of the tubing to move in one direction in a pulsating fashion but with an overall flow rate that is constant and regulated by the rate of pulsation and the tubing diameter.

peritoneum the thin translucent membrane, consisting of a single layer of flattened mesothelial cells and fibrous connective tissue, that lines the abdominal cavity and covers most of the viscera. —**peritoneal** *adj.*; **peritoneally** *adv.*

perlecan *another name for* **heparan sulfate proteoglycan core protein**. *See also* **syndecan**.

permeability **1** the quality or degree of being permeable or porous. **2** *or* **magnetic permeability** (of a substance) *symbol*: μ; the ratio of the **magnetic induction**, B, to the magnetic field strength, H, at any point within the substance, i.e. $\mu = B/H$. The SI unit is the henry per metre or newton per square metre.

permeability coefficient a measure of the ability of a specified permeant to diffuse across a permeability barrier. It is expressed as the amount of substance of the permeant passing through a unit area of the barrier in a unit time when a unit difference in amount-of-substance concentration is applied across it.

permeability of vacuum *symbol*: μ_0; a fundamental physical constant, of value $4\pi \times 10^{-7}$ H m^{-1} exactly.

permeabilize *or* **permeabilise** to render permeable. In cell biology, agents such as **saponin**, streptolysin O (*see* **streptolysin**), or an applied electric field are used to open holes in the plasma membrane of cells. —**permeabilization** *or* **permeabilisation** *n.*

permeable capable of being permeated; pervious.

permeant **1** able to permeate or to diffuse into or through. **2** a substance having such properties.

permease *(sometimes)* any protein or protein system that effects a catalytic, stereospecific transfer of a substrate across a biological membrane.

permeate to pass through, or cause to pass through, by diffusion; to pervade. —**permeation** *n.*

permeation chromatography any form of chromatography in which a permeable stationary phase is used and in which separation of the components of a mixture is based mainly upon selective exclusion effects, such as differences in molecular size and/or shape (in **molecular-sieve chromatography**) or differences in charge (in **ion-exclusion chromatography**). *See also* **gel-permeation chromatography**.

permissible allowable. —**permissibility** *n.*; **permissibly** *adv.*

permissive **1** allowing; tolerant. **2** *(in virology)* describing a line or strain of cells that allows replication of a specified infecting virus with consequent cell lysis. **3** *(in genetics)* describing a condition, e.g. temperature, or set of conditions that permits the growth of a conditional lethal mutant (*see* **conditional lethal mutation**). —**permissiveness** *n.*; **permissively** *adv.*

permissive temperature *see* **temperature-sensitive mutation**.

permittivity *see* **relative permittivity**.

permselective selectively permeable to certain (classes of) molecular entities.

permutation **1** the process or act of permuting. **2** any of the possible arrangements of the members of a specified set of conditions, numbers, residues, etc.

permute to change the sequence or arrangement of.

Permutit *a proprietary name for* ion-exchange materials and equipment utilizing **permutites**.

permutite any of a class of artificial zeolite ion-exchangers.

pernicious anemia *or (esp. Brit.)* **pernicious anaemia** a form of anemia characterized by defective production of erythrocytes and the presence of megaloblasts in the bone marrow, and sometimes accompanied by neurological changes. It is caused by a deficiency of vitamin B_{12} due either to a dietary deficiency of the vitamin or to a failure of production of **intrinsic factor**.

per os *Latin* by mouth; used especially to denote the administration of drugs, etc. by the oral route.

peroxidase **1** any oxidoreductase enzyme of the sub-subclass EC 1.11.1. These act on hydrogen peroxide as (electron) acceptor with the formation of water. **2** *the recommended name of* the enzyme EC 1.11.1.7, a hemoprotein that catalyses the reaction of hydrogen peroxide with a wide variety of donors, i.e.

$$\text{donor} + H_2O_2 = \text{oxidized donor} + 2\ H_2O.$$

Apart from removing H_2O_2, it participates in the oxidation of toxic reductants and in lignin metabolism. In plants there are isoforms in different tissues. Example, peroxidase C2 precursor from horseradish: database code PER2_ARMRU, 347 amino acids (37.99 kDa); the enzyme consists of the region from amino acid 25 to the end. —**peroxidatic** *adj.*

peroxidase–antiperoxidase *abbr.*: PAP; a soluble complex of horseradish **peroxidase** (def. 2) and an antibody to this peroxidase, used in immunochemical procedures in conjunction with specific primary and bridging second antibodies to give a sensitive method of detecting complementary antigens enzymatically.

peroxide **1** *(in inorganic chemistry)* **a** the O_2^{2} ion. **b** any member of a class of metallic oxides, such as sodium peroxide, Na_2O_2, that contain the peroxide ion and generate hydrogen peroxide on acidification. The name is sometimes used erroneously for certain higher oxides that do not contain the O_2^{2-} ion; e.g. lead peroxide (lead(IV) oxide, PbO_2), manganese peroxide (manganese(IV) oxide, MnO_2), nitrogen peroxide (nitrogen(IV) oxide, NO_2 or N_2O_4). **c** *short for* hydrogen peroxide, H_2O_2; an oxidizing agent. **2** *(in organic chemistry)* **a** any compound of general formula R′–O–O–R″, where the groups R′ and R″ are two chains, two rings, or a ring and a chain, and including cases when R′ = R″; e.g. ethyl phenyl peroxide, benzoyl (strictly, dibenzoyl) peroxide. In hydrogen peroxide, R′ = R″ = H. **b** *see* **hydroperoxide**.

peroxisomal bifunctional enzyme a monomeric peroxisomal enzyme (mainly in kidney and liver) with the activities of three steps in the **beta-oxidation system**. Example from human: database code ECHP_HUMAN, 722 amino acids (79.12 kDa). The domain comprising amino acids 1–128 has two enzyme activities: **enoyl-CoA hydratase** and **3,2-*trans*-enoyl-CoA isomerase**; the domain 280–571 has **3-hydroxyacyl-CoA dehydrogenase** activity, and 720–722 is the microbody targeting signal.

peroxisome a type of **microbody** that is rich in enzymes that act on or generate hydrogen peroxide, especially the enzymes catalase, (*S*)-2-hydroxy-acid oxidase, and D-amino-acid oxidase. Peroxisomes have been found in mammalian kidney and liver, and in yeasts and certain protozoans. They are particularly numerous in leaf photosynthetic cells of plants photosynthesizing via the Calvin (C_3) pathway; in plants they are closely associated with chloroplasts and mitochondria, which is consistent with their function in **photorespiration**. —**peroxisomal** *adj.*

peroxo+ *prefix (in inorganic chemical nomenclature)* indicating substitution (in the corresponding acid) of an –OH group by the –O–OH group; e.g. peroxomonosulfuric acid, HO–SO_2–O–OH.

peroxoacid *(in inorganic chemistry)* any acid that contains the –O–OH group. *Compare* **peroxy acid**.

peroxy+ *prefix or infix (in carboxylic-acid nomenclature)* indicating substitution of the –OH group in the carboxyl group by the –O–OH group; e.g. peroxypropionic acid, CH_3–CH_2–CO–O–OH. *See also* **per+** (def. 2c).

peroxy acid *(in organic chemistry)* any acid that contains the –CO–O–OH group. *Compare* **peroxoacid**.

peroxyformic acid *see* **performic acid**.

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perpendicular dichroism *see* **dichroic ratio**.

Perrin, Jean Baptiste (1870–1942), French physicist; Nobel Laureate in Physics (1926) 'for his work on the discontinuous structure of matter, and especially for his discovery of sedimentation equilibrium'.

persalt any salt of a **peroxoacid** or a **peroxy acid**.

perseitol D-*glycero*-D-*galacto*-heptitol; a substance found in avocado and the alligator pear.

perspective formula a type of **projection formula** in which the bonds of (a part of) a molecule tend to be depicted with increasing boldness according to their nearness to the viewpoint, and vice versa, in order to give an impression of perspective. *See* **Haworth representation**, **Mills perspective representation**.

Perspex *a proprietary name for* **poly(methyl methacrylate)**.

pertactin *other name*: outer membrane protein P68; an agglutinogen of *Bordetella* spp. that binds to eukaryotic cells, and is involved in the pathogenicity in whooping cough. It contains the **RGD** sequence motif. Example (precursor) from *Bordetella bronchiseptica*: database code PERT_BORBR, 911 amino acids (93.89 kDa).

perturb to cause a selective and measurable change in the state of equilibrium of a system, or in its associated properties, through the action or influence of a specific external agent; to undergo perturbation. —**perturbable** *adj.*

perturbant an agent (capable of) causing perturbation.

perturbation **1** the action or process of perturbing; an instance of this. **2** the condition of being perturbed. **3** a cause or factor of disturbance; perturbant.

pertussis toxin a mixture of proteins produced by *Bordetella pertussis*, the bacterium responsible for whooping cough in young children. The toxin causes long-lasting activation of G_i protein (*see* **G-protein**) through catalysing ADP-ribosylation of the α subunit. It contains the NAD-dependent ADP ribosyltransferase (EC 2.4.2.–). The toxin enzyme contains five chains (S1–S5) organized in two functional subunits, A and B. Subunit A comprises S1, which has the enzymic activity, and irreversibly uncouples the GTP-binding proteins G_i and **transducin** from their membrane receptors. Subunit B binds to the membrane receptors; it has the composition $S2S3S5S4_2$, dimers of S2S4 and S3S4 being held together by S5. The database codes of the five chains, S1–S5, are as follows: TOX1_BORPE, 269 amino acids (29.94 kDa); TOX2_BORPE, 226 amino acids (24.80 kDa); TOX3_BORPE, 227 amino acids (24.96 kDa); TOX4_BORPE, 152 amino acids (16.52 kDa); TOX5_BORPE, 133 amino acids (14.48 kDa).

Perutz, Max Ferdinand (1914–), Austrian-born British molecular biologist; Nobel Laureate in Chemistry (1962), the prize being shared with J. C. Kendrew 'for their studies on the structures of globular proteins' (actually hemoglobin and myoglobin).

pervaporate to vaporize a liquid from one side of a semipermeable membrane with which it is in contact on the other side, as a means of concentrating a solution or suspension in that liquid. —**pervaporation** *n.*

pervious permeable.

PEST hypothesis the hypothesis that the presence of one or more regions rich in proline (P), glutamic acid (E), serine (S), and threonine (T) in the primary structure of a protein confers susceptibility to rapid intracellular proteolysis.

pesticide any substance, natural or artificial, used to kill pests.

PET *abbr. for* positron emission tomography; *see* **tomography**.

peta+ *symbol*: P; SI prefix denoting 10^{15} times.

PETG *abbr. for* polyethyleneterephthalate glycol; a plastic developed as an alternative to PVC for use in packaging; in contrast to PVC it does not produce chloride fumes when burned, giving off only CO_2 and H_2O. Flexible, clear, robust, and light, it is also suitable for contact with food, since no plasticizers or stabilizers are used in its manufacture.

petite **1** describing a strain of yeast (or other) cells derived from a spontaneous mutant in which certain respiratory enzymes are defective or deficient, with consequent very slow growth and formation of unusually small colonies. **2** describing such a colony or mutant.

Petri dish *or* **Petri plate** a shallow, flat-bottomed, circular dish, usually of glass or transparent plastic and 5–15 cm in diameter, with a loosely fitting, overlapping cover. It is used especially for plate cultures of bacteria and moulds on solid (gelled) media, and for tissue culture. [After Richard Julius Petri (1852–1921), German bacteriologist.]

petroselaidic acid *see* **octadecenoic acids**.

petroselenate *numerical symbol*: 18:1(6); *the trivial name for Z*-octadec-6-enoate; a component of the fatty-acid hydrolysate of umbelliferous seed oils.

petroselenic acid *see* **octadecenoic acids**.

pFc′ fragment a protein fragment obtained (together with **F(ab′)$_2$ fragment**) by pepsin hydrolysis of an immunoglobulin molecule. That from human IgG is a 27 kDa protein, which is a noncovalently bonded dimer consisting of the C-terminal moieties of the heavy chains, and resembles the **Fc fragment** without the residues containing the linking disulfide bond.

PFP *abbr. for* pore-forming peptide *or* pore-forming protein; the term embraces cytotoxic peptides such as staphylococcal δ-toxin, **alamethicin**, **magainins**, and **cecropins**; pore-forming proteins include staphylococcal α-toxin, **streptolysin-O**, cnidarian toxins, **perforin**, and **aerolysin**.

PFK *abbr. for* phosphofructokinase.

pg *symbol for* picogram (i.e. 10^{-12} gram).

p*G* *symbol for* titration p*K*.

PG *abbr. for* **1** phosphatidylglycerol. **2** prostaglandin. **3** protegrin.

PGA *abbr. for* **1** phosphoglyceric acid. **2** pteroylglutamic acid. **3** prostaglandin A; *see* **prostaglandin**.

PGAH$_4$ *abbr. for* tetrahydropteroylglutamic acid.

PGAM *abbr. for* phosphoglycerate mutase.

PGB *abbr. for* prostaglandin B; *see* **prostaglandin**.

PGD *abbr. for* **1** phosphogluconate dehydrogenase (EC 1.1.1.43). **2** prostaglandin D (*see* **prostaglandin**).

PGE *abbr. for* prostaglandin E; *see* **prostaglandin**.

PGF *abbr. for* prostaglandin F; *see* **prostaglandin**.

PGF synthase *abbr. for* prostaglandin-F synthase.

PGG *abbr. for* prostaglandin G (*see* **prostaglandin**).

PGH *abbr. for* prostaglandin H (*see* **prostaglandin**).

PGH synthase *see* **prostaglandin-endoperoxide synthase**.

PGI *abbr. for* prostaglandin I (i.e. **prostacyclin**).

PGK *abbr. for* phosphoglycerate kinase.

P glycoprotein *or* **MDR protein** **1** a glycoprotein associated with drug resistance; it is a transmembrane ATP-dependent transporter that pumps hydrophobic substances out of cells. Drug-resistant cells demonstrate increased expression of the P-glycoprotein gene as one mechanism for their resistance to, e.g., chemotherapeutic anticancer drugs. *See also* **MDR**.

PGT *(in clinical chemistry) abbr. for* phosphoglucomutase.

pH a dimensionless quantity notionally defined as the negative decadic logarithm of the molal activity of hydrogen ions in a solution. Since the activity of a single species of ion is not measurable, pH is defined operationally according to the equation:

$$\mathrm{pH(X)} = \mathrm{pH(S)} + (E_s - E_x)F/(RT\ln 10)$$

where pH(S) and pH(X) are the pH values of a standard solution, S, and of the test solution, X, respectively; F is the Faraday constant, R the gas constant, and T the thermodynamic temperature; and E_s and E_x are, respectively, the electromotive forces of the two galvanic cells:

reference electrode | KCl (conc.) ¦¦ soln. S | H_2(g) | Pt,

and

reference electrode | KCl (conc.) ¦¦ soln. X | H_2(g) | Pt,

both cells being at the same temperature, with identical reference electrodes and bridge solutions, KCl (aq, $m \geq 3.5$ mol kg^{-1}). A **pH standard** solution, S, is chosen from a set of five

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covering the range pH 3.5 to pH 9, an assigned value of pH(S) at the required temperature being obtained from published tables. To a good approximation, the hydrogen electrodes in the two cells may be replaced by other hydrogen-ion-responsive electrodes, such as glass or quinhydrone electrodes. Originally pH was considered as the negative decadic logarithm of the molar concentration of hydrogen ions, a practice retained to the present day as representing a convenient approximation.

pH* *a notation commonly used to denote* the apparent pH of a solution containing ^2H_2O (i.e. D_2O), as measured electrometrically using a glass electrode without correction for the isotope effect on the electrode.

Ph *symbol for* the phenyl group.

PH-30 *or* **PH30** a sperm surface protein with **disintegrin** and metalloprotease domains. Example from *Cavia cobaya* consists of two subunits, α and β; α subunit: database code CCPH30ASP, 804 amino acids (86.81 kDa); β subunit: database code CCPH30BSP, 735 amino acids (81.81 kDa).

PHA *abbr. for* phytohemagglutinin (def. 1).

pH-activity profile *or* **pH profile** a plot of enzyme activity against pH, over a range in which the activity is reversibly affected by pH.

phaeo+ *an alternative spelling (esp. Brit.) of* **pheo+**.

phaeochromocytoma *an alternative spelling (esp. Brit.) of* **pheochromocytoma**.

phaeofarnesin *an alternative spelling (esp. Brit.) of* **pheofarnesin**.

phaeophorbide *an alternative spelling (esp. Brit.) of* **pheophorbide**.

phaeophytin *an alternative spelling (esp. Brit.) of* **pheophytin**.

phage *abbr. for* bacteriophage.

phage conversion *an alternative name for* **bacteriophage conversion**.

phage display library a special example of a gene library encoding fusion proteins of a foreign polypeptide sequence and a coat protein of phage M13 or (more usually) the closely related phage fd. When cloned, the phage is then said to display the foreign protein (in the coat proteins). There are two common versions of the technique. In one, the library consists of random oligonucleotides (e.g. 7-mers). Clones expressing oligopeptides that react with a specific antibody can then be selected using the antibody. In the other version, the library consists of oligonucleotides encoding a range of single-chain variable-domain antibodies. This approach is used where an antibody is required for an oligopeptide, which can thus be used to detect appropriate clones.

phage immunity the immunity conferred on a **lysogenic bacterium** by the presence of a **prophage** and a consequence of the expression of a gene such as *c*I in **lambda phage**.

phage induction *or* **prophage induction** the stimulation of prophage in lysogenic bacteria to enter the vegetative state. It is accomplished by the action of UV light, X-rays, nitrogen mustards, etc.

phage lambda *see* **lambda phage**.

phagemid a chimeric phage–plasmid **cloning vector** containing origins of both double-stranded and single-stranded replication. *See also* **phasmid**.

phage T4 an icosahedral DNA-containing **bacteriophage** that infects *Escherichia coli*. Its single molecule of double-stranded DNA is 174 kb in length. Various enzymes prepared from this phage are commonly used in genetic engineering; these include ligase, polymerase, and polynucleotide kinase.

phage typing a procedure for classifying bacteria according to their susceptibility to various bacteriophages.

phagocyte any cell that characteristically engulfs particles from its surroundings into its cytoplasm by **phagocytosis**. —**phagocytic** *adj.*

phagocytosis a type of endocytosis whereby certain cells – phagocytes – can engulf external particulate material by extension and fusion of pseudopods around each particle. The particles are initially contained within phagocytic vacuoles (**phagosomes**), which then fuse with primary lysosomes to effect digestion of the particles. Phagocytosis is employed by certain cells of the immune system, notably macrophages and neutrophils, to engulf and destroy target cells, tissue debris, and other particles, and by amoeboid protozoans. *Compare* **pinocytosis**.

phagolysosome an organelle formed by the fusion of a **phagosome** and a **lysosome**. Immediately after fusion there is a brief rise in the pH of the phagolysosome and neutral proteases and cationic proteins are active. Subsequently the pH falls and acid proteases become active. Indigestible substances remain in the phagolysosomes forming residual bodies.

phagosome an inclusion in a eukaryotic cell that arises from the ingestion of particulate material by **phagocytosis**. The phagosomes subsequently fuse with **lysosomes** to form a **phagolysosome**.

phalloidin *see* **phallotoxin**.

phallotoxin any member of a family of closely related bicyclic heptapeptides present in the highly poisonous agaric fungus, *Amanita phalloides*, commonly called the death-cap fungus or deadly agaric, and in some related species; **phalloidin** is the best-known member. All phallotoxins but one are toxic, though not as intensely so as the congeneric and much more slowly acting **amatoxins**; high doses of phalloidin in mice or rats cause death in a few hours. The common elements of the molecular structure of phallotoxins include residues of *cis*-4-hydroxy-L-proline, a D-amino acid (which is either threonine or β-hydroxyaspartic acid), and the bisfunctional amino acid, L-tryptathionine (which forms a thioether bridge across the molecule). The majority of phallotoxins bind specifically to F actin and so prevent its depolymerization to G actin; by this means the turnover of microfilaments is blocked and cell movement thereby inhibited.

pharmaceutic *an alternative name for* **pharmaceutical** (def. 2).

pharmaceutical **1** of, or pertaining to, drugs or pharmacy. **2** *or* **pharmaceutic** any medicinal substance, mixture, or formulation. —**pharmaceutically** *adv.*

pharmaceutics *an alternative name for* **pharmacy** (def. 1).

pharmaco+ *comb. form* indicating a drug or drugs.

pharmacodynamics *functioning as sing.* the branch of pharmacology dealing with the effects of drugs on the body, i.e. with the physiological, therapeutic, and toxicological responses to drugs with particular regard to the extent and time course of such effects. —**pharmacodynamic** *adj.*; **pharmacodynamically** *adv.*

pharmacogenetics *functioning as sing.* the branch of pharmacology dealing with the genetic mechanisms underlying individual differences in responses to drugs. —**pharmacogenetic** *adj.*; **pharmacogenetically** *adv.*

pharmacognosy the study of crude drugs of natural origins. —**pharmacognostic** *adj.*

pharmacokinetics *functioning as sing.* the branch of pharmacology dealing quantitatively with the movement of drugs within the body, i.e. with the absorption, distribution, metabolism, and elimination of drugs. —**pharmacokinetic** *adj.*; **pharmacokinetically** *adv.*

pharmacological *or (esp. US)* **pharmacologic** **1** of, pertaining to, or used in pharmacology. **2** (of an effect of a naturally occurring agonist) caused by an unphysiological concentration; (of a concentration or dose of a naturally occurring agonist) having an unphysiological effect. —**pharmacologically** *adv.*

pharmacology the science or study of drugs – their origin, characteristics, identification, biological effects, and modes of action. *Distinguish from* **pharmacy**.

pharmacopoeia *or (US, sometimes)* **pharmacopeia** **1** an authoritative book, often an official one, containing descriptions of medicinal drugs with their uses, preparation, methods of assay, formulae, dosages, etc. **2** the whole range of medicinal drugs in use or available. —**pharmacopoeial** *or* **pharmacopoeic** *adj.*

pharmacy **1** *or* **pharmaceutics** the practice of preparing and

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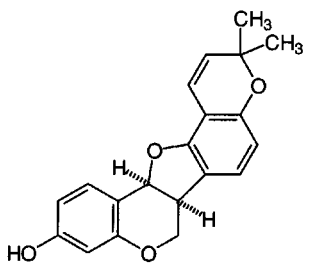
dispensing drugs. **2** a dispensary (for drugs). *Distinguish from* **pharmacology**.

phase **1** any distinct or characteristic period or stage in a sequence of events, occurrences, or processes, whether cyclical or unidirectional; e.g. the phases in the life cycle of an organism or the phases of the **cell-division cycle** (*see also* **anaphase**, **gap phase**, **metaphase**, **prophase**, **telophase**). **2** *(in physical science)* **a** the totality of those parts of a heterogeneous material system that are identical in chemical composition and physical state, and that are separated by an interface from the rest of the system; e.g. solid, liquid, or vapour phases, or the discrete phases into which immiscible liquids separate after mixing, etc. *See also* **epiphase**, **hypophase**, **liquid-crystalline phase**, **phase transition**. **b** a particular stage in the cycle of a periodic phenomenon, process, or quantity; the fraction of such a cycle that has been completed at a specific reference time, expressed in circular measure (or its equivalent in angular degrees). Two or more waveforms (or two or more similar sequences of events, etc.) that are in corresponding phases at the same time are described as 'in phase', while ones not exhibiting such correspondence are described as 'out of phase'. —**phasic** *adj.*

phase-contrast microscopy *or* **phase microscopy** a form of light microscopy in which a colourless object having a different refractive index from that of the medium is viewed by converting differences in refractive index into visible differences in light intensity. The technique takes advantage of the quarter-wave retardation of the illuminating light that occurs on its diffraction by the object, imposes a similar change of phase on the undiffracted light, and forms an image by interference between the two beams of light.

phaseolin **1** a crystallizable globulin found in seeds of the kidney bean, or French bean, *Phaseolus vulgaris*, and the lima bean, *Phaseolus lunatus*. It is a major seed-storage protein. α and β types are known. Example, α type precursor from *P. vulgaris*: database code PHSA_PHAVU, 436 amino acids (49.27 kDa). **2** *a former name for* **phaseollin**. **3** *an alternative name for* **legumain**.

phaseollin *or (formerly)* **phaseolin** a fungitoxic **phytoalexin** produced by plants of the kidney (or French) bean, *Phaseolus vulgaris*, and some other species of bean. It is a phenolic fused heterocyclic compound, $C_{20}H_{18}O_4$.



phase rule a generalization, valuable in the study of equilibria between **phases** (def. 2), expressed by the equation:

$$F = C - P + 2$$

where C is the number of chemically distinguishable components present, P is the number of phases in equilibrium, and F is the number of degrees of freedom of the system, i.e. the number of independently variable intensive properties that must be specified in order to describe completely the state of the system.

phaseshift mutation *an alternative term for* **frameshift mutation**.

phase transition (of lipids) the transition of a lipid between any of the various phases it can adopt. The transition is dependent on factors such as temperature, purity of the lipid, state of hydration, and, if not pure, the composition of the mixture. In the nonhydrated state, a crystalline polar lipid can on heating, prior to a complete melting, adopt a **liquid-crystalline phase**, in which the polar groups are still associated in sheets, so that the overall structure consists of lipid bilayers, but the fatty-acyl chains undergo increased thermal vibrations leading to considerable disorder; the temperature at which this transition occurs is known as the **phase-transition temperature**. In the presence of water, below the phase-transition temperature, phospholipids adopt a gel phase, in which water penetrates between the sheets of polar headgroups, but the fatty-acyl chains are highly ordered. On increasing the temperature through the phase-transition temperature, the lipid adopts a hydrated liquid-crystalline phase with disordered fatty-acyl chains. The term **fluidity** has been used to provide a qualitative description of these changes, the bilayer being said to become more fluid as the temperature increases. *See also* **hexagonal phase**.

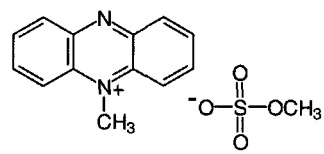
phase variation (of flagellin) *see* **flagellin**.

phasmid **1** a gene-cloning vector consisting of an artificial combination of a plasmid with a phage such that its genome contains functional origins of replication of both; it may thus be propagated either as a plasmid or as a phage in appropriate host strains. A phasmid is formed by insertion of one or more plasmid molecules into a phage genome. *Compare* **cosmid**, **phagemid**. **2** either of a pair of lateral caudal organs characteristic of parasitic nematodes of the class Phasmidia; they are thought to function as chemoreceptors. **3** any plant-eating insect of the order Phasmida, which includes leaf insects and stick insects.

PH domain *abbr. for* pleckstrin homology domain.

Phe *symbol for* a residue of the α-amino acid L-phenylalanine (alternative to F).

phenazine methosulfate *abbr.*: PMS; *N*-methylphenazonium methosulfate; 5-methylphenazinium methyl sulfate; $[C_{13}H_{11}N_2]^+$ $[CH_3SO_4]^-$; an artificial electron carrier, $E^{o\prime}$ = +0.080 V, useful in the study of redox enzyme systems.



phencyclidine 1-(1-phenylcyclohexyl)piperidine (*abbr.*: PCP); a potent psychotomimetic agent, known to drug users as angel dust, with analgesic and anesthetic actions. It acts as a ligand for the **sigma receptor** and is a blocker of the NMDA-receptor ionophore (*see* **glutamate receptor**). A controlled substance in the US Code of Federal Regulations.

phene any phenotypic character under genetic control.

phenelzine β-phenylethylhydrazine, (2-phenethyl)hydrazine; a nonselective monoamine oxidase inhibitor used as an antidepressant.

phenobarbital 5-ethyl-5-phenylbarbiturate; a major **barbiturate** drug.

phenocopy a nonhereditary modification of the phenotype of an organism, induced by nutritional or other environmental factors, that mimics a phenotype controlled by a specific gene.

phenol **1** *the common and trivial name for* hydroxybenzene, C_6H_5OH. **2** any compound containing one or more hydroxyl groups directly attached to an aromatic carbocycle. Unlike hydroxyalkyl compounds, phenols are weakly acidic.

phenolase **1** *an alternative name for* **catechol oxidase** (EC 1.10.3.1). **2** *an alternative name for* **monophenol monooxidase** (EC 1.14.18.1). **3** more loosely, any of various other enzymes of the sub-subclass 1.10.3. Such enzymes cause browning of damaged plant tissues when they come into contact with flavonoids, as **catechins** are converted into polymerized brown products.

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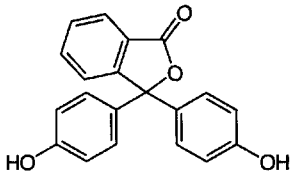
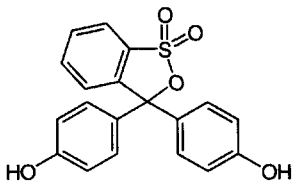
phenolic 1 of, containing, derived from, or having the character of phenol or a phenol. 2 describing a hydroxyl group linked to an aromatic carbocycle.

phenol 2-monooxygenase *see* **monooxygenase**.

phenolphthalein an indicator dye that changes from colourless to red over the pH range 8.3–10.0. The β-D-glucuronide (λ_{max} = 420 nm) is used as a substrate for the assay of β-glucuronidase, hydrolysis leading to release of phenolphthalein, which can be measured in alkaline solution by its red colour (λ_{max} = 550 nm).



Phenol Red an indicator dye that changes colour from yellow to red over the pH range 6.8–8.4.



phenome the whole of the phenotypic characteristics of an organism. *Compare* **genome**. —**phenomic** *adj.*

phenomenology a branch of a science dealing with the description and classification of natural phenomena rather than with their explanation or cause. —**phenomenological** *adj.*

phenon any set of organisms grouped together by the methods of numerical taxonomy.

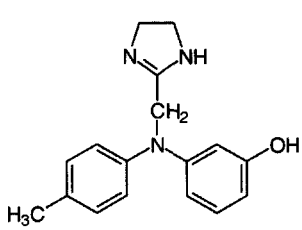
phenothiazine 1 a chemical structure that forms the basis, by *N*-substitution, of a group of **neuroleptics**, such as **chlorpromazine**. 2 any of the group of drugs based on the phenothiazine structure. The neuroleptic effects are those now most commonly exploited, but antiemetic, antihistamine and anthelmintic effects have also been of use.

phenotype 1 the totality of the observable functional and structural characteristics of an organism as determined by interaction of the genotype of the organism with the environment in which it exists. 2 any particular characteristic or set of characteristics of an organism so determined. 3 a group of organisms exhibiting the same set of such characteristics. *Compare* **genotype**. —**phenotypic** *adj.*

phenoxide 1 the anion, $C_6H_5O^-$, derived from phenol by the loss of a proton. 2 any salt of phenol.

phenoxy *symbol*: OPh *or* PhO; the C_6H_5O– group, derived from phenol by the loss of a hydrogen atom.

phentolamine an antagonist for both α_1 and α_2 adrenoceptors. It is an antihypertensive agent and vasodilator.

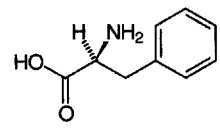


phenyl *symbol*: Ph; the aromatic carbocyclic group C_6H_5–, derived from benzene.

phenylacetaldehyde dehydrogenase EC 1.2.1.39; an enzyme of the pathway of phenylalanine degradation. It catalyses the oxidation by NAD^+ of phenylacetaldehyde to phenylacetate with formation of NADH.

phenylalaninate 1 phenylalanine anion; the anion, C_6H_5–CH_2–$CH(NH_2)$–COO^-, derived from **phenylalanine**. 2 any salt containing phenylalanine anion. 3 any ester of phenylalanine.

phenylalanine *the trivial name for* β-phenylalanine; α-amino-hydrocinnamic acid; α-amino-β-phenylpropionic acid; 2-amino-3-phenylpropanoic acid; C_6H_5–CH_2–$CH(NH_2)$–COOH; a chiral α-amino acid. L-phenylalanine (*symbol*: F *or* Phe), (*S*)-2-amino-3-phenylpropanoic acid, is a coded amino acid found in peptide linkage in proteins; codon: UUC or UUU. In mammals it is an essential dietary amino acid and is both glucogenic and ketogenic. Residues of D-phenylalanine (*symbol*: D-Phe *or* DPhe), (*R*)-2-amino-3-phenylpropanoic acid, occur in a number of peptide antibiotics, e.g. bacitracin A, gramicidin S, polymyxins B_1 and B_2, and tyrocidins A, B, and C.



L-phenylalanine

L-phenylalanine ammonia-lyase EC 4.3.1.5; *systematic name*: L-phenylalanine ammonia-lyase; an enzyme, widely distributed in plants, that deaminates L-phenylalanine to *trans*-cinnamic acid, which is rapidly converted to **lignin**, a major polymer of the plant cell wall.

phenylalanine hydroxylase *see* **phenylalanine 4-monooxygenase**.

phenylalanine 4-monooxygenase EC 1.14.16.1; *systematic name*: L-phenylalanine,tetrahydrobiopterin:oxygen oxidoreductase (4-hydroxylating); *other names*: phenylalanine 4-hydroxylase; phenylalaninase. An enzyme that catalyses a reaction between L-phenylalanine, tetrahydrobiopterin, and dioxygen to form L-tyrosine, dihydrobiopterin, and H_2O. It is thus of major importance for the provision of L-tyrosine. Absence of the enzyme in humans leads to **phenylketonuria**. It is an iron protein. Example from human: database code DHPR_HUMAN, 244 amino acids (25.77 kDa).

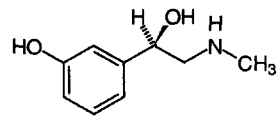
phenylalaninium phenylalanine cation; the cation, C_6H_5–CH_2–$CH(NH_3^+)$–COOH, derived from phenylalanine.

phenylalanino the alkylamino group, C_6H_5–CH_2–CH(COOH)–NH–, derived from phenylalanine.

phenylalanyl the acyl group, C_6H_5–CH_2–$CH(NH_2)$–CO–, derived from phenylalanine.

phenylalanyl chain *(sometimes)* the **B chain** of any of those species of insulin whose amino-acid sequences were the first to be determined. It was so called by virtue of the N-terminal phenylalanine residue occurring in those instances.

phenylephrine (*R*)-(–)-1-(3-hydroxyphenyl)-2-methylaminoethanol; a highly selective α_1 adrenergic agonist. It is a vasoconstrictor, used in treating hypotension; it also acts as a decongestant.



R-(–)-enantiomer

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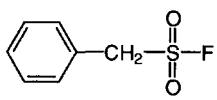
phenylethanolamine *N*-methyl transferase *abbr.*: PNMT; EC 2.1.1.28; an enzyme catalysing *N*-methylation of norepinephrine in the synthesis of epinephrine. *S*-adenosyl methionine is the methyl donor.

phenylhydrazone any condensation product of the type $R'R''C{=}N{-}NHC_6H_5$, formed between carbonyl compounds of the general formula $R'R''C{=}O$ and phenylhydrazine. Phenylhydrazones, in particular 2,4-dinitrophenylhydrazones, are useful in the characterization of aldehydes and ketones. *See also* **phenylosazone**.

phenylketonuria (*abbr.*: PKU) *or* **phenylpyruvic oligophrenia** an autosomal recessive inherited disorder of phenylalanine metabolism characterized by the presence of phenylpyruvate in the urine and excessively high levels of phenylalanine and its metabolites in the blood and tissues. It can be treated by restricting the amount of phenylalanine in the diet. If untreated in young children, severe mental retardation occurs. This form, **classical phenylketonuria**, is due to the absence or deficiency of **phenylalanine 4-monooxygenase**, an enzyme that uses tetrahydrobiopterin as second donor. Other types of hyperphenylalaninemia have been described due to, e.g., deficiency in dihydropteridine reductase (EC 1.6.99.7) or phenylalanine(histidine) aminotransferase (EC 2.6.1.58).

phenylmethylsulfonyl fluoride *or* **phenylmethanesulfonyl fluoride** *abbr.*: PMSF; a reagent used as an inhibitor of serine proteases; it is highly toxic, but less so than diisopropylphosphofluoridate. PMSF is both insoluble and unstable in aqueous solutions, so is usually added to such solutions by first dissolving it in, e.g., dioxan. It acts as an irreversible inhibitor of trypsin and chymotrypsin, sulfonylating the active-site histidine; it does not inhibit cholinesterase. *See also* **aminoethylbenzenesulfonyl fluoride**.



phenylosazone any 1,2-bis(phenylhydrazone); i.e. any condensation product of the type $C_6H_5NH{-}N{=}CR'{-}CR''{=}N{-}NH{-}C_6H_5$ formed between an α-dicarbonyl compound of the general formula $R'{-}CO{-}CO{-}R''$ and phenylhydrazine; α-hydroxy- and α-amino-carbonyl compounds will also form phenylosazones through oxidation of the corresponding [mono]phenylhydrazones initially formed. Phenylosazones, in particular 2,4-dinitrophenylosazones, are useful in the characterization of aldehydes and ketones, especially monosaccharides. *See also* **phenylhydrazone**.

phenylpropanoid any of a large and heterogeneous group of substances in plants derived from phenylpropane units variously linked and interlinked to form polymers of high molecular mass, especially **lignins**.

phenylpyruvate decarboxylase EC 4.1.1.43; an enzyme of the pathway of phenylalanine degradation. It catalyses the formation of phenylacetaldehyde from phenylpyruvate with release of CO_2.

phenylpyruvic oligophrenia *an alternative name for* **phenylketonuria**.

pH 5 enzyme *the provisional name given to* a protein fraction from rat liver, soluble at pH 7 and isolated by precipitation at pH 5, that was used in early studies of protein biosynthesis *in vitro*. It is now known to be a mixture of amino acid–tRNA ligases.

pheo+ *or (esp. Brit.)* **phaeo+** *comb. form* denoting dark-coloured.

pheochromocytoma *or (esp. Brit.)* **phaeochromocytoma** a tumour of tissues derived from embryological neuroectoderm, often of the adrenal medulla. It is characterized by its ability to synthesize and secrete catecholamines, often in excessive amounts. The tumour cells commonly show a strong **chromaffin** (*or* pheochrome) reaction.

pheofarnesin *or (esp. Brit.)* **phaeofarnesin** any pigment derived by demetallation of a chlorophyll in which the 17-propionic-acid group is esterified with farnesol.

pheophorbide *or (esp. Brit.)* **phaeophorbide** any pigment derived by removal of metal from a chlorophyll in which the 17-acrylic-acid or 17-propionic-acid group is unesterified or has been de-esterified.

pheophytin *or (esp. Brit.)* **phaeophytin** any pigment derived by removal of metal from a chlorophyll in which the 17-propionic-acid group is esterified with phytol.

pheromone a substance, or characteristic mixture of substances, that is secreted and released by an organism and detected by a second organism of the same or a closely related species, in which it causes a specific reaction, such as a definite behavioural reaction or a developmental process; a type of **ectocrine**. The mating pheromones of fungi and insects are examples. *Compare* **allomone**, **kairomone**.

pheromone-binding protein any of a group of insect proteins that bind to and thus solubilize **pheromones**, which are typically hydrophobic. Example (precursor) from the moth *Antherea polyphemus*: database code PBP_ANTPO, 163 amino acids (18.12 kDa) (first 21 amino acids are the signal).

pheromone receptor a fungal transmembrane G-protein-linked receptor. Example from *Ustilago maydis* (smut fungus), receptor for the A1 mating pheromone: database code PRA2_USTMA, 346 amino acids (38.74 kDa).

phi *symbol*: φ *or* ϕ (lower case) *or* Φ (upper case); the twenty-first letter of the Greek alphabet. For uses *see* **Appendix A**.

PHI *or* **PHI-27** *abbr. for* peptide HI.

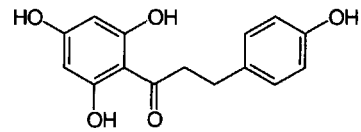
Philadelphia chromosome (Ph^1) a specific chromosomal abnormality in the blood cells of patients with chronic myeloid leukemia. It usually results from a fusion of ***BCR*** on chromosome 22 with c-*myc* (*see* ***MYC***) on chromosome 9 leading to expression of the latter. The Philadelphia chromosome is a very small chromosome consisting of the short arm and a small piece of the long arm of chromosome 22 fused to a short piece from the end of the long arm of chromosome 9 (the modified chromosome 9 that results being called 9q$^+$). It is named after the city in which it was first recorded. *See also* ***abl***.

pH indicator *see* **indicator** (def. 3), **mixed indicator**.

phi X174 *or* **φX174** a single-stranded DNA bacteriophage that infects *Escherichia coli*.

phloem the main food-conducting tissue of plants, via which nutrients and photosynthate are conveyed between different sites. Phloem comprises two types of cells: sieve-tube elements, which are joined end-to-end to form sieve tubes; and adjacent companion cells. *Compare* **xylem**.

phloretin 3-(4-hydroxyphenyl)-1-(2,4,6-trihydroxyphenyl)-1-propanone; the aglycon of **phlorizin**, with which it shares many biochemical and pharmacological properties.



phlorizin *or* **phlorhizin** *or* **phloridzin** *or* **phlorrhizin** phloretin-2′-β-glucoside; a dihydrochalcone glucoside occurring in all parts of the apple tree except the mature fruit. It is an inhibitor of intestinal and renal glucose–Na^+ cotransporters, of the mediated transport of glucose into erythrocytes and hepatocytes, of the glucose 6-phosphate transporter in hepatocytes, and of photophosphorylation. It is used experimentally to produce glucosuria.

phloroglucinol 1,3,5-trihydroxybenzene; 1,3,5-benzenetriol; a compound that is useful as a reagent for the qualitative detec-

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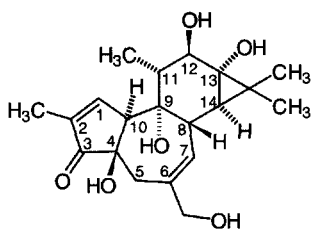
tion of pentoses and pentosans; when these are boiled with a solution of phloroglucinol in hydrochloric acid, a cherry-red colour is produced. Galactose also reacts in this way.

phlorrhizin *a variant spelling of* **phlorizin**.

pH meter any instrument for determining pH potentiometrically, usually with a glass electrode plus a calomel reference electrode, or with a combination electrode.

phorbol a complex tetracyclic compound, $C_{20}H_{28}O_6$, based on a cyclopropabenzazulene skeleton. Various **phorbol esters** occur in croton oil (from *Croton tiglium*, of the family Euphorbiaceae, hence the name) and act as potent **cocarcinogens**.



phorbol ester any esterified form of **phorbol**. A number of phorbol esters possess activity as tumour promoters and activate the mechanisms associated with cell growth. These actions have been widely attributed to the ability to activate protein kinase C, probably by substituting for diacylglycerol. A much-studied ester is phorbol 12-myristate 13-acetate (PMA); other active esters include phorbol 12,13-dibutyrate (PDBu) and phorbol 12,13-didecanoate (PDD). Activity depends on the β-configuration of the hydroxyl at C-4, and a number of 4α-phorbol esters have been utilized in control studies.

+phore *noun suffix* denoting something, especially a chemical substance or group, that carries or produces; e.g. *ionophore*, chromophore.

+phoresis *noun suffix* denoting carriage of molecular entities by some agency; e.g. electrophoresis, ionophoresis.

phosducin a part of a complex with the β and γ subunits of **transducin** in outer and inner segments of retinal rod cells. Light-induced changes in cyclic nucleotide levels modulate the phosphorylation of phosducin by cyclic AMP kinase. Example (bovine): database code PHOS_BOVIN, 245 amino acids (28.20 kDa).

+phosph+ *a variant form of* **+phospho+** (sometimes before a vowel).

phosphacan a chondroitin sulfate proteoglycan of brain that interacts with neurons and neural cell-adhesion molecules. It is an extracellular variant of a receptor-type protein tyrosine phosphatase. Example from rat: database code RNU04998, 1616 amino acids (175.65 kDa).

phosphagen any of a group of guanidine phosphates that occur in muscle and can be used to regenerate ATP from ADP during muscular contraction by a reaction catalysed by **creatine kinase** or by an analogous enzyme of sub-subclass EC 2.7.3. Included in the group are phosphoagmatine (*see* **agmatine**), **phosphoarginine**, **phosphocreatine**, phosphoglycocyamine (*see* **glycocyamine**), phospholombricine (*see* **lombricine**), phosphooctopine (*see* **octopine**), and phosphotaurocyamine (*see* **taurocyamine**).

phosphataemia *a variant spelling (esp. Brit.) of* **phosphatemia**.

phosphatase *or* **phosphomonoesterase** any phosphoric monoester hydrolase of sub-subclass EC 3.1.3. Some phosphatases are very specific while others are relatively unspecific with regard to substrate. *See also* **acid phosphatase**, **acylphosphatase**, **alkaline phosphatase**, **fructose-bisphosphatase**, **glucose-1-phosphatase**, **glucose-6-phosphatase**, **inorganic pyrophosphatase**, **protein phosphatase**.

phosphatased *a jargon term* indicating dephosphorylated by treatment with a **phosphatase**.

phosphatase inhibitor protein an inhibitor of protein phosphatase 1 (*see* **protein phosphatase**) involved in the regulation of glycolysis; it is itself a phosphoprotein. Example, inhibitor 1 from rat: database code IPP1_RAT, 171 amino acids (18.71 kDa).

phosphate **1** the trivalent anion, PO_4^{3-}, derived from phosphoric acid; orthophosphoric acid; tetraoxophosphoric(v) acid; $PO(OH)_3$. **2** any mixture of [ortho]phosphoric acid and its anions. Once widely used in the laboratory as a buffer in the physiological range of pH values; pK_{a2} (37 °C, 0.05 mol L^{-1}) = 6.84. **3** any (partial or full) salt or ester of [ortho]phosphoric acid. Phosphate salts and esters play key roles in the structure and function of all forms of life. **4** any anion or salt of a mixed anhydride of [ortho]phosphoric acid with another acid; e.g. acetyl phosphate (i.e. acetic phosphoric anhydride). **5** the univalent group $-O-P(O)(OH)_2$ (irrespective of its state of ionization). *See also* **diphosphate**, **inorganic phosphate**, ***metaphosphate***, ***pyrophosphate***, ***triphosphate***.

phosphate bond **1** an ester linkage in a phospho[mono]ester, phosphodiester, or phosphotriester. **2** an anhydride linkage in a phosphoric anhydride. **3** the connecting phosphoric residue in a phosphodiester.

phosphate bond energy *a term formerly and incorrectly used for* the **bond energy** (def. 2) of a **phosphate bond** (def. 1, 2).

phosphatemia *or (esp. Brit.)* **phosphataemia** the level of **phosphate** (def. 2) in the blood; in human plasma its normal range is 0.8–1.4 mmol L^{-1}. The level is regulated by **calcitriol**, which stimulates absorption of dietary phosphate as well as calcium, and by **parathyrin**, which decreases phosphate resorption by the kidney. Calcitriol also stimulates bone resorption, which tends to lower the plasma phosphate level, but in states of hypervitaminosis D the effect on the gut predominates and the plasma level is increased. *See also* **hyperphosphatemia**, **hypophosphatemia**.

phosphate potential the concentration of ATP in any system divided by the product of the concentrations of ADP and inorganic phosphate in that system. *Compare* **adenylate energy charge**.

phosphatidal *a former term for* **plasmenyl**.

phosphatidate any anion, salt, or ester of a **phosphatidic acid**.

phosphatidate cytidylyltransferase EC 2.7.7.41; *systematic name*: CTP:phosphatidate cytidylyl transferase; *other names*: CDPdiglyceride synthetase; CDPdiglyceride pyrophosphorylase. An enzyme that catalyses a reaction between CTP and phosphatidate to form pyrophosphate and CDPdiacylglycerol. It is an endoplasmic reticulum membrane-bound enzyme of phospholipid biosynthesis; it forms the intermediate involved in the synthesis of, e.g., phosphatidylinositol, by reaction with inositol, or phosphatidylserine, by reaction with serine. Example from *Escherichia coli*: database code CDSA_ECOLI, 249 amino acids (27.54 kDa).

phosphatidate phosphatase EC 3.1.3.4; *systematic name*: 3-*sn*-phosphatidate phosphohydrolase; an enzyme that removes phosphate from phosphatidic acid to yield an *sn*-1,2-diacylglycerol.

phosphatide *an old term, no longer recommended for* **glycerophospholipid**.

phosphatidic acid any derivative of glycerol phosphate in which both the remaining hydroxyl groups of the glycerol moiety are esterified with fatty acids; the commonest are derivatives of *sn*-glycerol 3-phosphate.

phosphatidyl *symbol*: Ptd; an acyl group derived from a **phosphatidic acid**.

phosphatidylcholine *abbr.*: PC; any of a class of glycerophospholipids in which a phosphatidyl group is esterified to the hydroxyl group of **choline**. They are important constituents of cell membranes and lipoproteins.

phosphatidylcholine desaturase EC 1.3.1.35; *other names*: oleate desaturase; linoleate synthase; an enzyme in plants that catalyses the reaction:

1-acyl-2-oleoyl-*sn*-glycero-3-phosphocholine + NAD^+ =

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1-acyl-2-linoleoyl-*sn*-glycero-3-phosphocholine + NADH.

phosphatidylcholine–dolichol *O*-acyltransferase *see* **lecithin–cholesterol acyl transferase**.

phosphatidylcholine–sterol *O*-acyltransferase EC 2.3.1.43; *other names*: lecithin–cholesterol acyltransferase (*abbr.*: LCAT); phospholipid–cholesterol acyltransferase; a plasma enzyme that catalyses the transfer of a fatty-acyl group from phosphatidylcholine to a sterol to form a sterol ester and 1-acylglycerophosphocholine. In mammals it is important in plasma lipoprotein metabolism, particularly in esterifying cholesterol, which is then transferred to very-low-density lipoprotein as cholesteryl ester. Example from human: database code LCAT_HUMAN, 440 amino acids (49.52 kDa). *Compare* **sterol *O*-acyltransferase**.

phosphatidylethanolamine *abbr.*: PE; any of a class of glycerophospholipids in which a phosphatidyl group is esterified to the hydroxyl group of **ethanolamine**. They are important constituents of cell membranes.

phosphatidylinositol *abbr.*: PI; *symbol*: PtdIns; 1-(3-*sn*-phosphatidyl)-1D-*myo*-inositol; *the recommended name for* any glycerophospholipid in which its *sn*-glycerol 3-phosphate residue is esterified to the 1-hydroxyl group of 1D-*myo*-inositol. The older term **phosphoinositide** is now used as a generic term for any inositol-containing glycerophospholipid. The corresponding names for the monophosphorylated and diphosphorylated derivatives of phosphatidylinositol are **phosphatidylinositol 4-phosphate** and **phosphatidylinositol 4,5-bisphosphate**, respectively. The older names diphosphoinositide and triphosphoinositide for these derivatives are no longer used.

phosphatidylinositol 4,5-bisphosphate *or (formerly)* **triphosphoinositide** *abbr.*: PIP_2 *or* PI-4,5-P_2; *symbol*: PtdIns(4,5)P_2 *or* PtdIns-4,5-P_2; 1-(3-*sn*-phosphatidyl)-1D-*myo*-inositol 4,5-bisphosphate; any of a class of glycerophospholipids in which a phosphatidyl group is esterified to the 1-hydroxyl group of 1D-*myo*-inositol 4,5-bisphosphate.

1-phosphatidylinositol-4,5-bisphosphate phosphodiesterase *see* **phospholipase**.

phosphatidylinositol cycle *or (formerly)* **phosphoinositide cycle** a metabolic cycle that mediates the actions of various hormones and other effectors at the membranes of mammalian cells. The cycle may be summarized as follows. Binding of an effector to its specific receptor at the cell membrane brings about a G-protein-coupled stimulation of a phospholipase C, of 1-phosphatidylinositol-4,5-bisphosphate phosphodiesterase. This action brings about hydrolysis of phosphatidylinositol 4,5-bisphosphate, I, to produce the two intracellular messengers inositol 1,4,5-trisphosphate, II, which causes release of calcium ions from intracellular stores, and *sn*-1,2-diacylglycerol, III, which activates protein kinase C. III is then converted via phosphatidate (under the action of **diacylglycerolkinase** and **phosphatidate cytidylyltransferase**) to **CDPdiacylglycerol**, IV, while II is converted via inositol bisphosphate and inositol monophosphate to inositol. Inositol and IV then react together (enzyme is **CDPdiacylglycerol-inositol 3-phosphatidyltransferase**) to form phosphatidylinositol, from which I is regenerated by stepwise phosphorylation by specific kinases to complete the cycle. Alternatively, II may be converted to another messenger, inositol 1,3,4,5-tetrakisphosphate, V, which may be implicated in the influx of extracellular calcium ions; V is then degraded to inositol via inositol 1,3,4-trisphosphate, which is inactive.

phosphatidylinositol glycan protein *abbr.*: PIG protein; *N*-acetylglucosaminyl-phosphatidylinositol biosynthetic protein; a protein required for synthesis of *N*-acetylglucosaminyl-phosphatidylinositol, the very early intermediate in the biosynthesis of the **GPI anchor**. Example, PIG-A (human): database code PIGA_HUMAN, 484 amino acids (54.06 kDa). Another protein required for this synthesis is PIG-F: database code PIGF_HUMAN, 219 amino acids (24.86 kDa).

1-phosphatidylinositol 3-kinase EC 2.7.1.137; *systematic name*: ATP:1-phosphatidyl-1D-*myo*-inositol 3-phosphotransferase. An enzyme that catalyses the phosphorylation by ATP of 1-phosphatidyl-1D-*myo*-inositol to form 1-phosphatidyl-1D-*myo*-inositol 3-phosphate with release of ADP. It forms part of the complex that associates on activation of certain growth factor (e.g. PDGF) receptors, binding via SH2 domains (*see* **SH domain**). The molecule is a heterodimer of a catalytic subunit (p110) and a regulatory subunit (p85: two forms, α and β, in mammals). p85 acts as an adaptor to mediate association of p110 to the plasma membrane. Examples, (bovine) p110: database code P11A_BOVIN, 1068 amino acids (124.18 kDa); p85(β): database code P85B_BOVIN, 724 amino acids (80.97 kDa).

1-phosphatidylinositol 4-kinase EC 2.7.1.67; an enzyme of the pathway for the biosynthesis of membrane **phosphoinositides**. It catalyses the phosphorylation by ATP of 1-phosphatidyl-1D-*myo*-inositol to form 1-phosphatidyl-1D-*myo*-inositol 4-phosphate with release of ADP. Example, α form (human): database code A55404, 854 amino acids (96.87 kDa).

phosphatidylinositol-3-phosphatase EC 3.1.3.64; an enzyme that catalyses the hydrolysis of the 3-phosphate from phosphatidylinositol-3-phosphate, forming phosphatidylinositol and orthophosphate.

phosphatidylinositol 4-phosphate *or (formerly)* **diphosphoinositide** *abbr.*: PIP *or* PI 4-P; *symbol*: PtdIns4*P or* PtdIns-4-*P*; 1-(3-*sn*-phosphatidyl)-1D-*myo*-inositol 4-phosphate; any of a class of glycerophospholipids in which a phosphatidyl group is esterified to the 1-hydroxyl group of 1D-*myo*-inositol 4-phosphate.

1-phosphatidylinositol-4-phosphate kinase EC 2.7.1.68; *other name*: diphosphoinositide kinase; an enzyme of the pathway for the biosynthesis of membrane **phosphoinositides**. It catalyses the phosphorylation by ATP of 1-phosphatidyl-1D-*myo*-inositol 4-phosphate to form 1-phosphatidyl-1D-*myo*-inositol 4,5-bisphosphate with release of ADP.

1-phosphatidylinositol phosphodiesterase *see* **phospholipase**.

phosphatidylinositol synthase *see* **CDP-diacylglycerol–inositol 3-phosphatidyltransferase**.

phosphatidylserine any of a class of glycerophospholipids in which a phosphatidyl group is esterified to the hydroxyl group of L-serine. They are important constituents of cell membranes.

phosphatidylserine decarboxylase EC 4.1.1.65; an enzyme that converts phosphatidylserine to phosphatidylethanolamine, of major importance in the synthesis of that phospholipid. It exists as a heterodimer of α and β chains, formed by cleavage of a proenzyme. Example, proenzyme from *Haemophilus influenzae*: database code DPSD_HAEIN, 290 amino acids (33.20 kDa); residues 1–256 form the β chain, 257–290 the α chain.

phosphatidylserine synthase *an alternative name for* **CDP-diacylglycerol-serine *O*-phosphatidyltransferase**.

phosphite **1** any anionic form of phosphorous acid; trioxophosphoric(III) acid; $P(OH)_3$. **2** any mixture of phosphorous acid and its ionized forms. **3** any (partial or full) salt or ester of phosphorous acid.

phosphite-triester method a method for the chemical synthesis of oligonucleotides in which a suitably protected phosphite diester of general formula Nuc-3′–O–P(OR)X, where R is a methyl or another alkyl group, X is a reactive group such as chloro, dimethylamino, or morpholino, and Nuc is a residue of an appropriate nucleoside, is first condensed with the 5′-hydroxyl of a protected nucleoside (usually anchored through its 3′-hydroxyl to an insoluble support) to form a phosphite triester. Sequential addition of further nucleoside units is then carried out in the same way, the phosphite triester formed at each stage being oxidized to the corresponding phosphate triester before the next cycle of reactions. Protecting groups are removed by hydrolysis at the completion of the synthesis.

+phospho+ *or (sometimes before a vowel)* **+phosph+** *(in chemi-*

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cal nomenclature) prefix or infix denoting a phosphoric residue linked to one, two, or three heteroatoms in an organic compound. *See also* **phospho-**.

phosphoacetylglucosamine mutase EC 5.4.2.3; *systematic name*: *N*-acetyl-D-glucosamine 1,6-phosphomutase; *other name*: acetylglucosamine phosphomutase. An enzyme that catalyses the reaction:

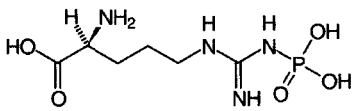
N-acetyl-D-glucosamine 1-phosphate = *N*-acetyl-D-glucosamine 6-phosphate.

It participates in the pathway for the formation of UDP-*N*-acetylglucosamine: glucosamine 6-phosphate → *N*-acetylglucosamine-6-phosphate →*N*-acetylglucosamine-1-phosphate, thence by reaction with UTP to UDP-*N*-acetylglucosamine + pyrophosphate, thence also to sialic acid. Example from *Schizosaccharomyces pombe*: database code PCM1_SCHPO, 518 amino acids (56.35 kDa).

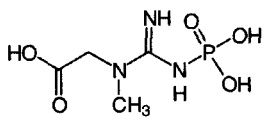
3′-phosphoadenosine 5′-phosphosulfate *an alternative recommended name for* **adenosine 3′-phosphate 5′-phosphosulfate**.

phosphoamino acid any phosphorylated amino acid. The term often refers to *O*-phosphate esters of residues in proteins, e.g. those of serine, threonine, or tyrosine, that are released as phosphoamino acids on hydrolysis. Phosphohistidine can be formed as part of an enzyme mechanism (e.g. **phosphoglycerate mutase**), and phosphohomoserine is an intermediate in threonine biosynthesis. The guanidine group can also be phosphorylated to form a phosphono derivative (*see* **phosphagen**).

phosphoarginine *the recommended trivial name for* **N^{ω}-phosphonoarginine**; the commonest **phosphagen** in invertebrates. The older name, arginine phosphate, is not recommended.



phosphocreatine *abbr.*: PC; *the recommended trivial name for* **N^{ω}-phosphonocreatine**; the commonest **phosphagen** in vertebrates. The older name, creatine phosphate, is not recommended.



phosphodiester any diester of phosphoric acid; i.e. any phosphoric ester containing the bridging group –PO(OH)– between two oxygen atoms in other groups (which may be the same or different) or at different positions in the same group. Examples include cyclic nucleotides, glycerophospholipids, and nucleic acids.

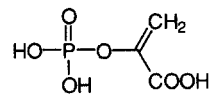
phosphodiesterase any esterase that catalyses the hydrolysis of either (but not both) of the ester linkages in a phosphodiester, each linkage being hydrolysed only by an enzyme specific for that linkage. Such enzymes are classified in various sub-subclasses within the subclass EC 3.1, hydrolases, especially in the sub-subclass EC 3.1.4, phosphoric diester hydrolases. The term is often applied to **nucleases** without sugar specificity. *See also* **cyclic AMP phosphodiesterase**, **phosphodiesterase I**, **phospholipase** C. —**phosphodiesteratic** *adj.*

phosphodiesterase I *the recommended name for* an enzyme, EC 3.1.4.1, that catalyses the hydrolytic removal of 5′-nucleotides successively from the (nonphosphorylated) 3′ end of an oligonucleotide; *other name*: 5′-exonuclease.

phosphodiesterase II *the former recommended name for* an enzyme, *now named* **spleen exonuclease** (EC 3.1.16.1; previously EC 3.1.4.18), that catalyses the hydrolytic removal of 3′-nucleotides successively from the (nonphosphorylated) 5′ end of a (preferably single-stranded) ribonucleic or deoxyribonucleic acid; *other names*: 3′-exonuclease; spleen phosphodiesterase.

phosphodiester method a method for the chemical synthesis of oligonucleotides in which, essentially, a 5′-phosphate of an appropriate [mono]nucleotide, after suitable protection of other functional groups, is condensed with the 3′-hydroxyl of a protected nucleoside, [mono]nucleotide, or previously formed oligonucleotide, using dicyclohexylcarbodiimide or an arylsulfonyl chloride as a coupling agent. The reaction sequence is then repeated with another nucleotide 5′-phosphate. This method is being superseded by the **phosphite-triester method** and **phosphotriester method**.

phospho*enol*pyruvate *abbr.*: PEP *or P-enol*pyruvate; 2-hydroxy-2-propenoate phosphate (ester); 2-(phosphonooxy)-2-propenoate; the phosphate ester formed from the hydroxy group of the enol tautomer of pyruvate. It is a so-called high-energy compound, hydrolysis to pyruvate giving a particularly large negative change in standard free energy ($-\Delta G^{\circ}$ = 62 kJ mol^{-1} at pH 7). It is a key intermediate in glycolysis and gluconeogenesis, and in the biosynthesis of aromatic amino acids.



phospho*enol*pyruvate carboxykinase *abbr.*: PEPCK; any of several enzymes that catalyse the reaction:

X–P + oxaloacetate = X + phospho*enol*pyruvate + CO_2,

where X–P, depending on source, can be GTP or ITP (in EC 4.1.1.32), ATP (in EC 4.1.1.49), or pyrophosphate (in EC 4.1.1.38). (1) **Phospho*enol*pyruvate carboxykinase (GTP)**, EC 4.1.1.32; *systematic name*: GTP:oxaloacetate carboxy-lyase (transphosphorylating); *other names*: phospho*enol*pyruvate carboxylase; phosphopyruvate carboxylase; the rate-limiting gluconeogenic enzyme in eukaryotes. It has different forms in cytoplasm and mitochondria. It catalyses a reaction between GTP and oxaloacetate to form GDP, phospho*enol*pyruvate, and CO_2. Example, mitochondrial precursor from chicken: database code PPCC_CHICK, 622 amino acids (69.45 kDa). (2) **Phospho*enol*pyruvate carboxykinase (ATP)**, EC 4.1.1.49; *systematic name*: ATP:oxaloacetate carboxy-lyase (transphosphorylating); *other names*: phospho*enol*pyruvate carboxylase; phosphopyruvate carboxylase (ATP); it catalyses a similar reaction to (1) but with ATP/ADP not GTP/GDP. In many bacteria it is a Ca^{2+}-regulated rate-limiting gluconeogenic enzyme. Example from *Escherichia coli*: database code PPCK_ECOLI, 464 amino acids (51.25 kDa). *See also* **gluconeogenesis**.

phospho*enol*pyruvate carboxylase EC 4.1.1.31; *systematic name*: orthophosphate:oxaloacetate carboxy-lyase (phosphorylating); an enzyme that catalyses a reaction between orthophosphate and oxaloacetate to form phospho*enol*pyruvate, H_2O, and CO_2. It is an allosteric enzyme associated with the **tricarboxylic-acid cycle** in plants; effectors include fatty acids, acetyl-CoA, and fructose 1,6-bisphosphate. It forms oxaloacetate for metabolism by the tricarboxylic-acid cycle in plants. The protein is a homotetramer. Example from *Escherichia coli*: database code CAPP_ECOLI, 883 amino acids (98.95 kDa).

phospho*enol*pyruvate-dependent sugar phosphotransferase system *abbr.*: PTS; a system for bacterial sugar transport, the full system comprises two main components:

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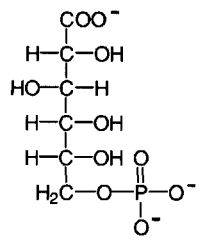

phosphogluconate

protein-*N*$^{\pi}$-phosphohistidine–sugar phosphotransferase and **phospho*enol*pyruvate–protein phosphotransferase**. The system functions also as a chemoreceptor monitoring the environment for changes in sugar concentration.

phospho*enol*pyruvate mutase EC 5.4.2.9; *systematic name*: phospho*enol*pyruvate 2,3-phosphonomutase; *other name*: phospho*enol*pyruvate phosphomutase. An enzyme that catalyses the conversion of phospho*enol*pyruvate to 3-phosphonopyruvate. Phospho*enol*pyruvate mutase is an enzyme of the pathway that synthesizes **bialaphos** forming the C–P bond in the phosphinothricin moiety. Example from *Streptomyces hygroscopicus*: database code BCPB_STRHY, 313 amino acids (33.66 kDa).

phospho*enol*pyruvate–protein phosphotransferase EC 2.7.3.9; *systematic name*: phospho*enol*pyruvate:protein-L-histidine N^{π}-phosphotransferase; *other name* enzyme I of the **phospho*enol*pyruvate-dependent sugar phosphotransferase system**; a soluble bacterial enzyme, part of a system for the transport of hexoses across the cell membrane, that catalyses the phosphorylation by phospho*enol*pyruvate of a low-M_r, heat-stable protein, **HPr**. Example from *Escherichia coli*: database code PT1A_ECOLI, 711 amino acids (78.30 kDa).

phosphoester any [mono]ester of phosphoric acid; i.e. any phosphoric ester containing the group $-PO(OH)_2$ linked to an oxygen atom in a single other group.

phosphofructokinase **1** *abbr.*: PFK; EC 2.7.1.11; *recommended name*: 6-phosphofructokinase; *other names*: phosphofructokinase 1; phosphohexokinase. An enzyme that catalyses the phosphorylation of D-fructose 6-phosphate to D-fructose 1,6-bisphosphate at the expense of ATP, CTP, ITP, or UTP.

Phosphofructokinase 1 is an allosteric glycolytic enzyme; the molecule is a homotetramer. Example from *Escherichia coli*: database code K6P1_ECOLI, 320 amino acids (34.72 kDa); 3-D structure known; this is isoenzyme I; *E. coli* has a second entirely unrelated isoenzyme (II), presumably of independent evolution.

2 *or* **phosphofructokinase 2** EC 2.7.1.105; *recommended name*: 6-phosphofructo-2-kinase; an enzyme that catalyses the phosphorylation of D-fructose 6-phosphate to D-fructose 2,6-bisphosphate at the expense of ATP. Phosphofructokinase 2 is the same protein as **fructose-2,6-bisphosphatase; phosphorylation** inhibits the kinase activity. Example from human (liver isoform; homodimer): database code F26L_HUMAN, 471 amino acids (54.64 kDa).

3 *or* **fructose-1-phosphate kinase** EC 2.7.1.56; *recommended name*: 1-phosphofructokinase; an enzyme that catalyses the phosphorylation of D-fructose 1-phosphate to D-fructose 1,6-bisphosphate at the expense of ATP, GTP, ITP, or UTP.

phosphoglucoisomerase *an alternative name for* **glucose-6-phosphate isomerase**.

phosphoglucomutase *abbr. (in clinical chemistry)*: PGT; EC 5.4.2.2; *systematic name*: α-D-glucose 1,6-phosphomutase; *other name*: glucose phosphomutase. A **phosphotransferase** enzyme that catalyses the interconversion of α-D-glucose 1-phosphate and α-D-glucose 6-phosphate; α-D-glucose 1,6-bisphosphate is an intermediate, formed by phosphoryl transfer from the enzyme. It is a key enzyme linking the metabolism of polysaccharides to glycolysis. Example from *Saccharomyces cerevisiae*: database code PGMU_YEAST, 570 amino acids (63.04 kDa).

phosphogluconate 6-phospho-D-gluconate; an intermediate in the **Entner–Doudoroff pathway** and in the **pentose phosphate pathway**. It is a product of the combined action of **glucose-6-phosphate dehydrogenase** and **6-phosphogluconolactonase**, and is a substrate for **phosphogluconate dehydrogenase (decarboxylating)**. (Illustrated opposite.)

phosphogluconate dehydrogenase (decarboxylating) *abbr.*: 6PGD; EC 1.1.1.44; *systematic name*: 6-phospho-D-gluconate:$NADP^+$ 2-oxidoreductase (decarboxylating); *other names*: phosphogluconic acid dehydrogenase; 6-phosphogluconic dehydrogenase; 6-phosphogluconic carboxylase. An enzyme that catalyses a reaction between 6-phospho-D-gluconate and $NADP^+$ to form D-ribulose 5-phosphate, CO_2, and NADPH. It is an important enzyme in the **pentose phosphate pathway**, and is significant in maintaining $NADP^+$ in the reduced state. Example from *Escherichia coli*: database code 6PGD_ECOLI, 468 amino acids (51.48 kDa).

phosphogluconate (oxidative) pathway *an alternative name for* **pentose phosphate pathway**.

6-phosphogluconolactonase EC 3.1.1.31; *systematic name*: 6-phospho-D-glucono-1,5-lactone lactonohydrolase; an enzyme of the **pentose phosphate pathway** that accelerates the rate of hydrolysis of 6-phosphogluconolactone to 6-phosphogluconic acid.

phosphoglycerate **1** 2-phospho-D-glycerate; D-glycerate 2-phosphate; (*R*)-2,3-dihydroxypropanoate 2-(dihydrogen phosphate). **2** 3-phospho-D-glycerate; D-glycerate 3-phosphate; (*R*)-2,3-dihydroxypropanoate 3-(dihydrogen phosphate). These phosphoglycerates are important intermediates in glycolysis. 3-phosphoglycerate is a precursor in serine biosynthesis. *Compare* **glycerophosphate**, **phosphoglyceride**. *See also* **phosphoglycerate mutase**.

phosphoglycerate dehydrogenase EC 1.1.1.95; *systematic name*: 3-phosphoglycerate:NAD^+ 2-oxidoreductase; an enzyme that converts 3-phospho-D-glycerate to 3-phosphohydroxypyruvate in the presence of NAD^+. An enzyme in the pathway for the synthesis of serine from 3-phosphoglycerate. Example from *Bacillus subtilis*: database code SERA_BACSU, 419 amino acids (45.60 kDa).

phosphoglycerate kinase *abbr.*: PGK; EC 2.7.2.3; *systematic name*: ATP:3-phospho-D-glycerate 1-phosphotransferase; an enzyme that catalyses the phosphorylation of of 3-phospho-D-glycerate by ATP to 3-phospho-D-glyceroyl phosphate with release of ADP. Phosphoglycerate kinase is important in the glycolytic pathway, and exists in tissue-specific or (in protozoa, etc.) organelle-specific isoforms. Example from wheat chloroplast: database code PGKY_WHEAT, 401 amino acids (42.07 kDa).

phosphoglycerate mutase *abbr.*: PGAM; EC 5.4.2.1; *systematic name*: D-phosphoglycerate 2,3-phosphomutase; *other names*: phosphoglycerate phosphomutase; phosphoglyceromutase. An enzyme of the glycolytic and gluconeogenic pathways that catalyses the reaction:

2-phospho-D-glycerate = 3-phospho-D-glycerate

(the forward direction, as written, being the direction in which the enzyme functions in gluconeogenesis). A phosphotransferase enzyme for which 2,3-bisphospho-D-glycerate acts as a reaction primer. The active enzyme has a phosphoryl group active site (histidine is phosphorylated as part of the mechanism) and transfers phosphoryl to the substrate. Example

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from *Saccharomyces cerevisiae*: database code PMGY_YEAST, 246 amino acids (27.45 kDa). *See also* **phosphohistidine**.

phosphoglycerate phosphomutase *another name for* **phosphoglycerate mutase**.

3-phospho-D-glyceric phosphoric monoanhydride *see* **3-phospho-D-glyceroyl phosphate**.

phosphoglyceride *another (less correct) name for* **glycerophospholipid**.

3-phospho-D-glyceroyl phosphate *abbr.*: D-glyceric-1,3-P_2; *one of the recommended names for* (*R*)-[2,3-dihydroxypropanoyl dihydrogen phosphate 3-(dihydrogen phosphate)], a key intermediate in the glycolytic pathway, commonly but incorrectly known as 1,3-diphosphoglycerate or 1,3-bisphosphoglycerate. *Alternative recommended names*: 3-phospho-D-glyceric phosphoric monoanhydride; (D-glyceroyl phosphate) 3-phosphate. This compound should be distinguished from **2,3-bisphospho-D-glycerate**.

phosphohexose isomerase *an alternative name for* **glucose-6-phosphate isomerase**.

phosphohistidine N^{π}-phosphohistidine; it is formed as a residue in certain proteins; being an intermediate in the **phosphoglycerate mutase** reaction and the **phospho*enol*pyruvate-dependent sugar phosphotransferase system**.

phosphoinositide *another old term, no longer recommended, for* **phosphatidylinositol** but now much used to denote all phosphatidylinositol derivatives as a class.

phosphoinositide cycle *another term for* **phosphatidylinositol cycle**.

phosphoketolase EC 4.1.2.9; a thiamine diphosphate-protein of the phosphoketolase pathway that catalyses phosphorolysis of D-xylulose 5-phosphate and orthophosphate to acetyl phosphate and D-glyceraldehyde 3-phosphate.

phosphoketolase pathway any metabolic pathway, usually in a microorganism, that involves the enzyme **phosphoketolase**, e.g. in **heterolactic fermentation** or in the fermentation of glucose by *Bifidobacterium* spp.

phosphokinase *a former term for* **kinase**.

phospholamban a homopentameric sarcoplasmic reticulum membrane protein that regulates the calcium pump of cardiac, slow-twitch skeletal, and smooth muscle. It is phosphorylated by protein kinase A in response to β-adrenergic stimulation. The phosphorylated protein increases the rate of the sarcoplasmic reticulum Ca^{2+}-ATPase. Example from human: database code PPLA_HUMAN, 52 amino acids (6.10 kDa).

phospholemman a 72-residue cell-membrane protein that forms a chloride-selective ion channel. It is a substrate for both protein kinase C and cyclic AMP-dependent protein kinase. It is rapidly phosphorylated after β-adrenergic and α-adrenergic stimulation of the heart and in response to insulin in muscle. It has a single transmembrane domain. The structure of a related protein, Mat-8, expressed in human breast tumours, is known: database code A55571, 87 amino acids.

phospholipase any enzyme that is a lipase and that catalyses the hydrolysis of a glycerophospholipid. Phospholipases have been subdivided as follows.

Phospholipase A_1 EC 3.1.1.32; *the recommended name for* any carboxylic ester hydrolase that removes the acyl residue at C-1 of the glycerol moiety.

Phospholipase A_2 *the recommended name for* any carboxylic ester hydrolase that removes the acyl residue at C-2 of the glycerol moiety; e.g. EC 3.1.1.4; *systematic name*: phosphatidylcholine 2-acylhydrolase; *other names*: lecithinase A; phosphatidase; phosphatidolipase. The enzyme requires calcium. Snake-venom enzymes have been much studied and have broad specificity for phosphoglyceride classes. There are two such mammalian enzymes, the pancreatic type and the membrane-bound type. The pancreatic enzyme is released from the exocrine pancreas on stimulation by cholecystokinin, has broad specificity for phosphoglycerides, and hydrolyses phospholipids of digested food in the intestine in conjunction with the action of bile salts to form micelles. The membrane-bound enzyme is instrumental in releasing arachidonate for prostanoid synthesis, and is in many cases stimulated by activated hormone and growth-factor receptors. Example, precursor from human (pancreatic enzyme): database code PA2M_HUMAN, 144 amino acids (16.06 kDa), 3-D structure known.

Phospholipase B EC 3.1.1.5; *recommended name*: lysophospholipase; *other names*: lecithinase B; lysolecithinase. These are enzymes that remove the acyl group from a lysoglycerophospholipid.

Phospholipase C *abbr.*: PLC; *the recommended name for* any phosphoric diester hydrolase that splits the bond between the phosphorus atom and the oxygen atom at C-1 of the glycerol moiety; *other names*: lipophosphodiesterase I; lecithinase C; *Clostridium welchii* α-toxin. Two major types have been studied; one is a bacterial type, which acts on phosphatidylcholine, releasing diacylglycerol (EC 3.1.4.3); there is also a mammalian enzyme of this type. The other type, **1-phosphatidylinositol phosphodiesterase** (EC 3.1.4.10) acts on phosphoinositides; it is found in bacteria and animals, and catalyses the conversion of 1-phosphatidyl-D-*myo*-inositol to D-*myo*-inositol 1,2-cyclic phosphate (which is hydrolysed in animals but not bacteria to inositol 1-phosphate) and diacylglycerol; **1-phosphatidylinositol-4,5-bisphosphate phosphodiesterase** (EC 3.1.4.11; *other names*: triphosphoinositide phosphodiesterase; phosphoinositide-specific phospholipase C) catalyses the hydrolysis of 1-phosphatidyl-D-*myo*-inositol 4,5-bisphosphate to D-*myo*-inositol 1,4,5-trisphosphate and diacylglycerol. These enzymes play a role in signal transduction. There are at least six forms of the latter, which is required for production of the second messenger molecules **diacylglycerol** and **inositol 1,4,5-trisphosphate**. The activation involves a G_{α} **G-protein** subunit. Example, PLC β_2 from human: database code PIP2_HUMAN, 1181 amino acids (133.53 kDa).

Phospholipase D EC 3.1.4.4; *the recommended name for* any phosphoric diester hydrolase that splits the bond between the phosphorus atom of a glycerophospholipid and the oxygen atom of the nitrogenous base; *other names*: lipophosphodiesterase II; lecithinase D; choline phosphatase.

phospholipid *or (formerly)* **phospholipide** any lipid containing phosphoric acid as mono- or diester.

phospholipid–cholesterol acyltransferase *see* **phosphatidylcholine–sterol *O*-acyltransferase**.

phospholipid exchange protein any of a number of cytosolic proteins that bind phospholipids and transport them within the cell. Each type of protein exhibits a degree of specificity for the phospholipid bound, and each protein molecule carries one or two phospholipid molecules. These proteins function to exchange phospholipid classes between different intracellular membrane sites.

phospholipid translocase a type of protein that accelerates the transfer of phospholipid (*see* **flip-flop**) between the inner and outer lipid leaflets of the plasma membrane bilayer.

phosphomannomutase EC 5.4.2.8; *systematic name*: D-mannose 1,6-phosphomutase; an enzyme that catalyses the reaction:

D-mannose 1-phosphate = D-mannose 6-phosphate.

One of its functions is to convert mannose 6-phosphate to mannose 1-phosphate, from which GDPmannose is synthesized; this is a precursor of **fucose**, and is an intermediate in the synthesis of the **mannose** core of oligosaccharides. Example from *Escherichia coli*: database code CPSG_ECOLI, 456 amino acids (50.40 kDa).

phosphomonoester any monoester of phosphoric acid.

phosphomonoesterase **1** *an alternative name for* **phosphatase**. **2** *an alternative name for* either **acid phosphatase** or **alkaline phosphatase**.

phosphonic acid *see* **phosphono+**.

phosphono+ *comb. form* denoting a phosphonic residue, $-PO(OH)_2$, derived from **phosphonic acid**, $HPO(OH)_2$. In biochemical usage this name is usually reserved for the $-PO(OH)_2$

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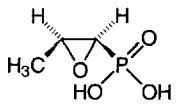
group attached to a carbon atom, as in **phosphonoacetate**, $(HO)_2OP–CH_2COO^-$; and **2-phosphonoethylamine**, or **ciliatine**, $(HO)_2OP–CH_2CH_2NH_2$; the group is commonly termed phospho+ when linked to a heteroatom, as in phosphocreatine and phosphogluconate.

N^{ω}-phosphonoarginine *see* **phosphoarginine**.

N^{ω}-phosphonocreatine *see* **phosphocreatine**.

phosphonomycin *or* **fosfomycin** (1*R*,2*S*)-(1,2-epoxypropyl)phosphonate; an antibiotic produced by *Streptomyces* and *Pseudomonas* strains. It binds irreversibly to UDP-*N*-acetylglucosamine 1-carboxyvinyl transferase (EC 2.5.1.7), an enzyme catalysing the first stage in the synthesis of bacterial cell-wall peptidoglycan from UDP-*N*-acetylglucosamine, which it thereby inhibits. It penetrates the cell by utilizing the L-α-glycerophosphate transport system. Loss of this system is a primary reason that resistant strains emerge.



phosphonopeptide any of a series of oligopeptide derivatives, designed as inhibitors of bacterial cell-wall biosynthesis, that have a C-terminal residue of L-1-aminoethylphosphonic acid (a phosphorus-containing analogue of L-alanine).

phosphopentomutase EC 5.4.2.7; *systematic name*: D-ribose 1,5-phosphomutase; *other name*: phosphodeoxyribomutase. An enzyme that catalyses the reaction:

D-ribose 1-phosphate = D-ribose 5-phosphate.

The partial sequence is known from *Escherichia coli*: database code DEOB_ECOLI.

phosphoprotein any protein containing one or more phosphoric residues directly attached, usually by ester linkage, to amino-acid residues.

phosphoprotein phosphatase **1** EC 3.1.3.16; *systematic name*: phosphoprotein phosphohydrolase; any enzyme that removes a phosphate group from a protein by hydrolysis. Many different enzymes have been identified with varying specificity with respect to the primary structure of the substrate protein. *See* **protein phosphatase**. **2** *another name for* **serine/threonine-specific protein phosphatase**.

phosphor any substance (capable of) exhibiting **phosphorescence** (def. 1).

phosphor+ *a variant form of* **phosphoro+** (before a vowel).

phosphoramidate *or* **amidophosphate** *or* **phosphoric amide** **1** any ion, salt, or ester of phosphoramidic acid; amidophosphoric acid; $(OH)_2PO–NH_2$. **2** any compound containing the group $(OH)_2PO–NH–$ or $(OH)_2PO–N<$.

phosphoramidite any compound having the general structure $R_3R_4NP(R_2)–O–R_1$. Phosphoramidites are useful in the synthesis of oligonucleotides or for the addition of groups to the 5′-phosphate of nucleotides or oligonucleotides. R_1 is often cyanoethyl-; R_3 and R_4 are often isopropyl with R_2 in 3′-nucleotide linkage.

phosphoramidon *N*-(α-L-rhamnopyranosyl-oxyphospho)-L-leucyl-L-tryptophan; a specific inhibitor of **thermolysin**. It is an inhibitor of the metalloendopeptidase, EC 3.4.24.11, that is responsible for cleaving and inactivating **natriuretic peptide**, with corresponding pharmacological effects.

phosphoresce to exhibit **phosphorescence** (def. 1).

phosphorescence **1** a type of luminescence consisting of the emission by a substance of electromagnetic radiation, especially visible light, as a result of the absorption of energy derived from exciting radiation of shorter wavelength or from incident subatomic particles (especially electrons or alpha particles), and that persists for more than approximately 10 ns after excitation ceases, the persistence being a consequence of the excited electrons decaying via a **metastable** (def. 2) state; the property of emitting such radiation. **2** the radiation so emitted. **3** *a common but erroneous term for* **bioluminescence** (which occurs in the absence of exciting radiation). *Compare* **fluorescence**. —**phosphorescent** *adj.*

phosphorescence spectrophotometry measurement of the wavelengths and the intensities of the light emitted from a phosphorescent sample that is excited by monochromatic (or nearly so) exciting radiation.

phosphori+ *a variant form of* **phosphoro+** (def. 3).

phosphoriboisomerase *see* **ribose-5-phosphate epimerase**.

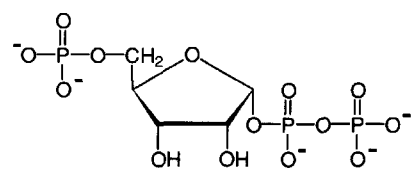
phosphoribosylamine–glycine ligase EC 6.3.4.13; *other names*: phosphoribosylglycinamide synthetase; glycinamide ribonucleotide synthetase (*abbr.*: GARS); an enzyme of the pathway for *de novo* purine biosynthesis that catalyses the reaction between ATP, 5′-phosphoribosylamine, and glycine to form 5′-phosphoribosylglycinamide (glycinamide ribotide, *abbr.*: GAR) with release of ADP and orthophosphate. Example from *Bacillus subtilis*: database code PUR2_BACSU, 422 amino acids (45.23 kDa). Example from human: database code PUR2_HUMAN, 1010 amino acids (107.64 kDa). This multifunctional protein has domains for three proteins required for purine biosynthesis (amino-acid numbers in brackets): GARS (1–433), **phosphoribosylformylglycinamidine cycloligase** (434–809), and **phosphoribosylglycinamideformyl-transferase** (810–1010), although variations with only one or two of the domains occur through alternative splicing.

phosphoribosylaminoimidazolecarboxamide formyltransferase EC 2.1.2.3; *other name*: AICAR transformylase; inosinicase; IMP synthetase; an enzyme of the pathway for *de novo* **purine biosynthesis** that catalyses the formation of 5′-phosphoribosyl-5-formamido-4-imidazolecarboxamide from 10-formyltetrahydrofolate and 5′-phosphoribosyl-5-amino-4-imidazolecarboxamide (5-aminoimidazole-4-carboxamide ribotide; *abbr.*: AICAR) forming also tetrahydrofolate. Example, multifunctional protein from chicken having activities for AICAR transformylase and **IMP cyclohydrolase**: database code PUR9_CHICK, 593 amino acids (64.34 kDa). The IMP cyclohydrolase activity resides in the C-terminal region.

phosphoribosylaminoimidazole carboxylase EC 4.1.1.21; *other name*: AIR carboxylase; an enzyme of the pathway for *de novo* purine biosynthesis that catalyses the formation of 1-(5′-phosphoribosyl)-5-amino-4-imidazolecarboxylate from 1-(5′-phosphoribosyl)-5-aminoimidazole (5′-aminoimidazole ribotide, *abbr.*: AIR) and CO_2. The reaction requires neither biotin nor ATP. For an example, *see* **multifunctional protein ade2**.

phosphoribosylaminoimidazolesuccinocarboxamide synthase EC 6.3.2.6; *other name*: SAICAR synthetase; an enzyme that catalyses the formation of 1-(5′-phosphoribosyl)-4-(*N*-succinocarboxamide)-5-aminoimidazole (*N*-succinylo-5-aminoimidazole-4-carboxamide ribonucleotide; *abbr.*: SAICAR) from ATP, 1-(5′-phosphoribosyl)-4-carboxy-5-aminoimidazole and L-aspartate with release of ADP and orthophosphate. The reaction forms part of the pathway for the *de novo* synthesis of purines. For an example, *see* **multifunctional protein ade2**.

(5-)phospho(-α-D-)ribosyl diphosphate *symbol*: *PP*Rib*P* *or* *P*Rib*PP*; 5-phospho-α-D-ribofuranosyl diphosphate; α-D-ribose 1-diphosphate 5-phosphate; a compound that is essential in the biosynthesis of various nitrogen-containing ring compounds or their derivatives, especially of histidine, and of purines and pyrimidines as their nucleotides. It is commonly but incorrectly known as phosphoribosyl pyrophosphate (*abbr. (not recommended)*: PRPP).



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phosphoribosylformylglycinamidine cyclo-ligase EC 6.3.3.1; *other name*: phosphoribosyliminoamidazole synthetase; an enzyme that catalyses the reaction between ATP and 2-formamido-N^1-(5-phosphoribosyl)acetamidine to form 1-(5-phosphoribosyl)-5-aminoimidazole with release of ADP and orthophosphate. Example from rabbit: database code A53688, 201 amino acids (22.71 kDa).

phosphoribosylformylglycinamidine synthase EC 6.3.5.3; *other names*: phosphoribosylformylglycinamidine synthetase; FGAM synthase; an enzyme of the pathway for *de novo* purine biosynthesis that catalyses the formation of 5′-phosphoribosylformylglycinamidine from ATP, 5′-phosphoribosylformylglycinamide, L-glutamine, and H_2O with release of ADP, orthophosphate, and L-glutamate. Example from yeast: database code PUR4_YEAST, 1360 amino acids (149.15 kDa).

phosphoribosylglycinamide formyltransferase EC 2.1.2.2; *other names*: 5′-phosphoribosylglycinamide transformylase; GAR transformylase (*abbr.*: GART); an enzyme of the pathway for *de novo* purine biosynthesis that catalyses the formation of 5′-phosphoribosyl-*N*-formylglycinamide (formylglycinamide ribotide; *abbr.*: FGAR) from 10-formyltetrahydrofolate and 5′-phosphoribosylglycinamide (glycinamide ribotide, *abbr.*: GAR) yielding also tetrahydrofolate. Example, multifunctional protein from chicken for **phosphoribosylamine–glycine ligase** (GARS)/**phosphoribosylformylglycinamidine cyclo-ligase** (AIRS)/GART: database code PUR2_CHICK, 1003 amino acids (106.42 kDa).

phosphoribosyl pyrophosphate *abbr.*: PRPP; *a common name for* **(5-)phospho(-α-D-)ribosyl diphosphate**.

phosphoribosyl pyrophosphate synthetase (*abbr.* PRS) *see* **ribose-phosphate pyrophosphokinase**.

phosphoribosyltransferase EC 2.4.2.7–2.4.2.12, 2.4.2.17; any of a group of enzymes that catalyse the biosynthesis of a mononucleotide from 5-phospho-α-D-ribosyl diphosphate (PRPP) in an alternative (or salvage) pathway for nucleoside biosynthesis. They catalyse a reaction between a base and 5-phospho-α-D-ribosyl diphosphate to form a D-ribonucleotide and pyrophosphate; the base may be (number indicates no. in sub-subclass EC 2.4.2) adenine (7), hypoxanthine (8), uracil (9), orotate (10), nicotinate (11), nicotinamide (12), or ATP (17). Examples: (1) hypoxanthine/guanine phosphoribosyltransferase (**HGPRT**) from human: database code HPRT_HUMAN, 217 amino acids (24.42 kDa); (2) ATP phosphoribosyltransferase, involved in histidine biosynthesis, from *Escherichia coli*: database code HIS1_ECOLI, 299 amino acids (33.33 kDa). Other phosphoribosyltransferases of sub-subclass EC 2.4.2 involve the following (no. in sub-subclass EC 2.4.2): anthranilate (18), dioxotetrahydropyrimidine (20), and xanthine (22).

phosphoric *symbol*: *P or* (in the one-letter convention for nucleotides) p; *the general name for* a residue of [ortho]phosphoric acid – i.e. tetraoxophosphoric(v) acid, $PO(OH)_3$ – whether singly, doubly, or triply attached to other groups and whether or not any residual hydroxyl groups are deprotonated.

phosphorimetry the measurement of **phosphorescence**.

phosphoro+ *or (before a vowel)* **phosphor+** *comb. form* **1** phosphorus. **2** [ortho]phosphoric acid. **3** *or* **phosphori+** phosphorescence.

phosphoroclastic describing a chemical reaction in which a carbon–carbon bond is split apparently by the action of inorganic phosphate with attachment of a phosphoric group to one of the resulting fragments.

phosphorolysis any reversible lytic process or reaction undergone by an acyl compound (I) or glycosyl compound (II) in which nucleophilic displacement by phosphate (anion) occurs, with formation of the corresponding acyl or sugar phosphate and uptake of a hydron by the other moiety of the original compound, as in the generalized equations:

(I) $R–CO–OR' + PO_4H_2^- + H^+ = R–CO–O–PO_3H_2 + HOR'$

or

(II) $R–O–R' + PO_4H_2^- + H^+ = R–O–PO_3H_2 + HOR'$.

phosphorolytic of, or relating to, phosphorolysis; capable of undergoing phosphorolysis.

phosphorous **1** of, containing, or resembling phosphorus. **2** a residue of phosphorous acid – i.e. trioxophosphoric(III) acid, $P(OH)_3$ – whether singly or doubly attached to other groups and whether or not any residual hydroxyl groups are deprotonated.

phosphorus *symbol*: P; a nonmetallic element of group 15 of the (IUPAC) **periodic table**; atomic number 15; relative atomic mass 30.974; it exists naturally as a single stable nuclide, **phosphorus-31**. Phosphorus occurs only in the combined state, almost exclusively as phosphates. Its commonest covalencies are III and V. Phosphorus compounds are vital components of all living materials. *See also* **phosphorus-32**, **phosphorus-33**.

phosphorus-31 the stable nuclide $^{31}_{15}P$; its relative abundance in natural phosphorus is 100 atom percent.

phosphorus-32 the artificial radioactive nuclide $^{32}_{15}P$. It emits a relatively high-energy electron or β^- particle (1.709 MeV max.) and no gamma radiation. It has a half-life of 14.3 days.

phosphorus-33 the artificial radioactive nuclide $^{33}_{15}P$. It emits a moderate-energy electron or β^- particle (0.249 MeV max.) and no gamma radiation. It has a half-life of 25.4 days.

phosphorus:oxygen ratio *abbr.*: P:O ratio; the number of atoms of inorganic phosphorus (as phosphate) incorporated into organic compounds (usually ATP) per atom of dioxygen consumed during **oxidative phosphorylation**. The value observed depends on the nature of the substrate being oxidized and the state of preservation of mitochondrial function. If the latter is high, a P:O ratio near 3 is observed during the oxidation of NADH, near 2 for succinate, fatty acyl CoA, 3-phosphoglycerate. *See also* **chemiosmotic coupling hypothesis**, **tight coupling**.

phosphoryl **1** the trivalent group –P(O)= derived from phosphoric acid. **2** *a name used frequently for* the univalent group $–P(O)(OH)_2$; this usage is not recommended; a phosphoric ester may be named, e.g., choline *O*-(dihydrogenphosphate) or *O*-phosphonocholine. However, phosphoryl is accepted except in derived terms such as the names of enzymes (e.g. phosphorylase) or processes (e.g. phosphorylation). *See also* **phosphono+**.

phosphorylase **1** *the name recommended for* any of various enzymes, classified together as EC 2.4.1.1, that catalyse the phosphorolytic removal of the nonreducing terminal glucose residue from a glucan according to the general reaction:

$$Glc\alpha1\text{-}[4Glc\alpha1\text{-}]_n4Glc + \text{orthophosphate} = Glc\alpha1\text{-}[4Glc\alpha1\text{-}]_{n-1}\text{-}4Glc + Glc\alpha1\text{-phosphate}.$$

These enzymes vary somewhat in regard to their preferred substrate; the name should be qualified in each instance by prefixing to it the name of the natural substrate (e.g. starch phosphorylase). Glycogen phosphorylase exists in two forms: **phosphorylase *a***, the more active, phosphorylated form; and **phosphorylase *b*** (*or* dephosphophosphorylase), the less active, unphosphorylated form. The conversion of *b* to *a* is effected with ATP by the enzyme **phosphorylase kinase**, and the conversion of *a* to *b* is brought about by the enzyme **phosphorylase phosphatase** (EC 3.1.3.17). Example from *Rattus norvegicus*, glycogen phosphorylase liver form: database code PHS1_RAT, 850 amino acids (97.48 kDa). **2** *a generic name recommended for* those glycosyltransferase enzymes within subclass EC 2.4 that utilize orthophosphate as acceptor. Some appear to be specific, e.g. maltose phosphorylase (EC 2.4.1.8) or uridine phosphorylase (EC 2.4.2.3), others less so, e.g. 1,3-β-oligoglucan phosphorylase (EC 2.4.1.30). *See also* ***α*-glucan phosphorylase**.

phosphorylase kinase EC 2.7.1.38; *systematic name*: ATP-

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phosphorylase-*b* phosphotransferase; *other name*: dephosphophosphorylase kinase. An enzyme that catalyses the reaction:

4 ATP + 2 phosphorylase *b* = 4 ADP + phosphorylase *a*.

Its activity is regulated by Ca^{2+}/calmodulin and by covalent modification, as a result of phosphorylation by **cyclic AMP-dependent protein kinase** or dephosphorylation by **protein phosphatase** 1. The enzyme has the subunit structure $\alpha_4\beta_4\gamma_4\delta_4$; of these γ is the catalytic chain, α and β are regulatory, and δ is a synonym for **calmodulin**. Example, γ chain (human): database code KPBH_HUMAN, 406 amino acids (46.39 kDa).

phosphorylase-limit dextrin the polysaccharide produced by the action of starch phosphorylase on the branched polysaccharide **amylopectin**.

phosphorylase phosphatase EC 3.1.3.17; an enzyme that catalyses the hydrolysis of phosphorylase *a* to two molecules of phosphorylase *b* and four of orthophosphate, thereby converting the phosphorylase to a less active form. *See also* **protein phosphatase**.

phosphorylate to effect **phosphorylation**.

phosphorylation the act or process of introducing a **phosphoric** group into a molecule, usually with the formation of a phosphoric ester, a phosphoric anhydride, or a phosphoric amide. Biochemical phosphorylation reactions are of importance in the trapping of energy and the formation of biosynthetic intermediates during metabolic processes and in the control of the activity of numerous enzymes and other proteins. *See also* **oxidative phosphorylation**, **photophosphorylation**, **substrate-level phosphorylation**.

phosphorylation state ratio *symbol*: R_p; a measure of the phosphorylating power of the adenylate system within cells. It is given by:

$$R_p = [ATP]/[ADP][P_i].$$

Compare **(adenylate) energy charge**.

phosphorylcholine–glyceride transferase *see* **diacylglycerol cholinephosphotransferase**.

phosphorylcholine transferase *see* **cholinephosphate cytidylyltransferase**.

phosphorylethanolamine transferase *see* **ethanolamine-phosphate cytidylyltransferase**.

phosphoryn the major phosphate-rich protein of **dentine**. It contains about 40 residue % of phosphoserine and 35 residue % of aspartic acid. It is isolated from incisors and is involved in bone mineralization. Soluble forms and a form complexed with collagen in dentine are known.

phosphoserine *O*-phospho-L-serine; a phosphoamino acid found in peptide linkage in proteins. Phosphorylation of serine and threonine residues is catalysed by protein kinases specific for serine or threonine residues, and phosphorylation and dephosphorylation mechanisms have a regulatory role in the protein function. *See also* **protein kinase**, **protein phosphatase**.

3-phosphoshikimate 1-carboxyvinyltransferase EC 2.5.1.19; *systematic name*: phospho*enol*pyruvate:3-phosphoshikimate 5-*O*-(1-carboxyvinyl)-transferase; *other name*: 5-*enol*pyruvyl shikimate-3-phosphate (EPSP) synthase; an enzyme of the **shikimate pathway** that catalyses the formation of O^5-(1-carboxyvinyl)-3-phosphoshikimate (5-*enol*pyruvyl shikimate 5-phosphate) from phospho*enol*pyruvate and 3-phosphoshikimate with release of orthophosphate. *See* **pentafunctional arom polypeptide**.

phosphosphingolipid *see* **sphingolipid**.

phosphothreonine *O*-phospho-L-threonine; a phosphoamino acid found in peptide linkage in proteins. Phosphorylation of serine and threonine residues is catalysed by protein kinases specific for serine or threonine residues, and phosphorylation and dephosphorylation mechanisms have a regulatory role in the protein function. *See also* **protein kinase**, **protein phosphatase**.

phosphotransferase any of the enzymes of sub-subclasses EC 2.7.1 to 2.7.4, and EC 2.7.9; they catalyse transfer of a phosphate group from a donor to an acceptor, and are classified according to whether the transfer is to an alcohol group (EC 2.7.1), a carboxyl group (EC 2.7.2), a nitrogenous group (EC 2.7.3), a phosphate group (EC 2.7.4) or to paired acceptors (EC 2.7.9 – only two of these are currently classified, transferring phosphate from ATP to both pyruvate and orthophosphate in one case and to pyruvate and water in the other, yielding AMP in both instances). Enzymes of sub-subclass EC 2.7.6 that transfer diphosphate are classified as **diphosphotransferases**.

phosphotransferase system a system for transferring substrates into bacteria (*see* **phospho*enol*pyruvate-dependent sugar phosphotransferase system**).

phosphotriester any triester of phosphoric acid.

phosphotriester method (of oligonucleotide synthesis) a method for the chemical synthesis of oligonucleotides in which a suitably protected phosphodiester of general formula Nuc–3′–O–P(O)(OR)OH, where R is an aryl group and Nuc is a residue of an appropriate nucleoside, is first condensed with the 5′-hydroxyl group of another nucleoside (usually anchored through its 3′-hydroxyl group to an insoluble support) to form a phosphotriester. Sequential addition of further nucleoside units is then carried out in the same way, the 5′-protecting group being removed at each stage before the next cycle of reactions. All remaining protecting groups are removed at the completion of the synthesis.

phosphotyrosine *O*-phospho-L-tyrosine; a phosphoamino acid found in peptide linkage in proteins, especially in proteins involved in effector mechanisms in growth stimulation, including growth-factor factor receptors. *See also* **protein kinase**, **protein phosphatase**.

phosphovitin *or* **phosvitin** a phosphoprotein (subunit size 25 kDa) that, together with **lipovitellin**, constitutes the major part of the mass of the egg-yolk proteins in oviparous vertebrates. It has the highest phosphorus content of all known phosphoproteins (10% P) and approximately half of its amino-acid residues are serine, all of which are *O*-phosphorylated. Phosphovitin and lipovitellin are derived from a common precursor protein, **vitellogenin**.

phot the cgs unit of illuminance, equal to one lumen per square centimetre; 1 phot = 10^4 lux.

phot+ *a variant form of* **photo+** (sometimes before a vowel).

photagogikon (*pl.* **photagogika**) the light-emitting compound of any luminescent system regardless of binding of the compound or of its state of ionization. *See also* **photogen**.

photic **1** of, or relating to, light. **2** of, or relating to, the reaction to light of, or the production of light by, living organisms. **3** describing the uppermost zone in a body of water that receives sufficient light to permit photosynthesis. —**photically** *adv.*

photo+ *or (sometimes before a vowel)* **phot+** *comb. form* denoting **1** of, pertaining to, produced by, or responding to light. **2** involving a photographic process.

photoactivate to render active or reactive by means of light. —**photoactivation** *n.*; **photoactivatable** *or* **photoactivable** *adj.*

photoactive *(of a substance)* capable of giving a physical or chemical response to light or other electromagnetic radiation.

photoaddition any chemical addition reaction promoted by light or other electromagnetic radiation.

photoaffinity label *or* **photolabel** an **affinity label** carrying a separate photoactivatable group that on illumination reacts with the protein being labelled to form a covalent link.

photoautotroph *or* **photolithotroph** any organism that is both an **autotroph** and a **phototroph**. —**photoautotrophic** *adj.*; **photoautotrophy** *n.*

photobiochemistry the photochemistry of biochemical processes. —**photobiochemical** *adj.*; **photobiochemically** *adv.*; **photobiochemist** *n.*

photobiology the study of the effects of radiation, mainly of visible and ultraviolet light, on living organisms. —**photobiological** *adj.*; **photobiologist** *n.*

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photobleaching the loss of colour or fluorescence through the action of incident visible or near-ultraviolet radiation.

photocatalysis **1** the acceleration of a chemical reaction by light. **2** the catalysis of a photochemical reaction. —**photocatalytic** *adj.*; **photocatalytically** *adv.*

photocathode *(in an electronic device)* a cathode from which electrons are emitted when exposed to electromagnetic radiation of suitable frequency.

photocell *or* **photoelectric cell** any type of transducer capable of converting incident electromagnetic radiation to an electric signal of corresponding magnitude. It may function by generating a potential difference or a current, or by changing its conductance.

photochemical action spectrum the relationship between the efficiency of a **photochemical reaction** and the frequency of the illuminating light.

photochemical reaction any chemical reaction that is initiated or accelerated by the absorption of visible or near-ultraviolet radiation.

photochemistry the branch of chemistry concerned with the effect of electromagnetic, especially visible and ultraviolet, radiation on chemical processes and with the uptake or production of photons during chemical reactions. —**photochemical** *adj.*; **photochemically** *adv.*

photochromism *or* **phototropy** the property possessed by certain substances of changing colour reversibly when exposed to electromagnetic radiation of appropriate frequency. *Compare* **electrochromism**, **thermochromism**. —**photochromic** *adj.*

photoconductive describing an electrical device that is capable of changing its conductance on exposure to light or other electromagnetic radiation. —**photoconductivity** *n.*

photodamage deleterious chemical change caused by the action of light, especially ultraviolet light.

photodensitometer *see* **densitometer** (def. 1).

photodetector a device, e.g. a **photocell**, that responds to incident light.

photodimerization *or* **photodimerisation** the formation of dimers by a photochemical reaction. It is of particular importance in the formation of **pyrimidine dimers** in DNA. —**photodimerize** *or* **photodimerise** *vb.*

photodiode any semiconductor **diode** (def. 1) that generates a potential difference or changes its conductivity when exposed to light.

photodissociation the splitting of a molecule into smaller molecules, radicals, or atoms on absorption of a quantum of electromagnetic radiation.

photodynamic involving, causing, or promoting a deleterious reaction to light, particularly ultraviolet light. Such reactions usually involve oxidation. Damage is caused by **singlet oxygen** produced, e.g., by illumination of chlorophyll in chloroplasts. Normally the singlet oxygen is quenched by the carotenoid pigments coexisting with the chlorophylls in chloroplasts. Hence, any mutation that deletes carotenoids from chloroplasts is lethal, because the chlorophylls are destroyed by singlet oxygen.

photoelectric of, pertaining to, or concerned with electric or electronic effects caused by electromagnetic radiation, especially light.

photoelectric cell *an alternative name for* **photocell**.

photoelectron an electron that is ejected from an atom on interaction of the atom with a photon of sufficient energy.

photoelectron micrograph any photograph of an object taken by **photoelectron microscopy**.

photoelectron microscopy an electron-microscopic technique in which **photoelectrons** emitted from a specimen exposed to ultraviolet radiation are accelerated and focused to produce an image. It is the counterpart in the electron microscope of fluorescence microscopy in the light microscope, the resolution being correspondingly enhanced.

photoelectron spectroscopy a technique in which a specimen (a gas sample or the surface of a solid or a liquid) is exposed to monochromatic electromagnetic radiation in the ultraviolet or X-ray regions and the energy spectrum of the emitted **photoelectrons** recorded. This provides information about the atomic composition of the specimen and also about the types of orbitals to which the constituent electrons of its atoms and molecules are assigned.

photoemission the emission of electrons from a surface as a result of bombardment by photons.

photoexcitation the act or process of raising an atom or molecule to a higher energy state by interaction with a photon.

photogen **1** *an older term for* **photagogikon**. **2** *a term proposed for* the specific biochemical precursor of a photagogikon.

photographic emulsion *or* **emulsion** any medium that is sensitive to light or other electromagnetic radiation, used for preparing photographic film, paper, etc., and consisting usually of a suspension of a silver salt (especially the bromide or chloride) in gelatin; a coating of such a suspension applied to a substrate.

photoheterotroph *or* **photoorganotroph** any organism that is both a **heterotroph** and a **phototroph**. —**photoheterotrophic** *adj.*; **photoheterotrophy** *n.*

photoinactivation the irreversible abolition of specific biological activity by the action of light.

photoinhibition the reversible abolition of specific biological activity by the action of light.

photoionization *or* **photoionisation** the ionization of a molecular entity by the loss of an electron on interaction of the entity with a photon of sufficient energy.

photokinesis any change in the undirected movement of an organism in response to variation in light intensity. —**photokinetic** *adj.*

photolabel *an alternative term for* **photoaffinity label**.

photolabile (of a substance) unstable in the presence of light.

photolithotroph *an alternative term for* **photoautotroph**. —**photolithotrophic** *adj.*; **photolithotrophy** *n.*

photoluminescence luminescence as a result of absorption of electromagnetic radiation. The emitted light is always of lower frequency than that of the incident radiation. —**photoluminescent** *adj.*; **photoluminesce** *vb.*

photolyse *or (sometimes, US)* **photolyze** to subject to or to undergo **photolysis**.

photolysis the cleavage of one or more covalent bonds in a molecular entity resulting from absorption of energy from light or other electromagnetic radiation; any photochemical process in which such a cleavage is an essential part, e.g. laser photolysis; flash photolysis. —**photolytic** *adj.*; **photolytically** *adv.*

photolyze *a US spelling of* **photolyse**.

photometer any instrument used to measure the intensity of light or other electromagnetic radiation; includes **spectrophotometer**.

photometry the measurement of the intensity of light or other electromagnetic radiation; it includes spectrophotometry (*see* **spectrophotometer**). —**photometric** *adj.*; **photometrically** *adv.*

photomicrograph a photograph taken through a light microscope; it is sometimes, incorrectly, termed a microphotograph. —**photomicrographic** *adj.*; **photomicrographically** *adv.*; **photomicrography** *n.*

photomultiplier a photocell consisting of a **photocathode** linked to an **electron multiplier**. Photons striking the photocathode cause the emission of electrons, which are then amplified by the electron multiplier to give an enhanced signal.

photon *symbol (in nuclear reactions, etc.)*: γ; a quantum of light (or other electromagnetic radiation) considered as a particle with zero rest mass, zero charge, and energy $h\nu$ joule, where h is the Planck constant and ν the frequency of the radiation in hertz.

photon counter a device, consisting of a photomultiplier and an associated scaler, that is capable of responding to and recording individual photons.

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photonicking photolysis of a nucleic-acid molecule with production of a **nick**.

photoorganotroph *an alternative term for* **photoheterotroph**. —**photoorganotrophic** *adj.*; **photoorganotrophy** *n.*

photooxidize *or* **photooxidise** to oxidize by the use of, or as a result of, radiation in the visible and ultraviolet wavelengths. —**photooxidizable** *or* **photooxidisable** *adj.*

photoperiod **1** the length of daylight in a 24-hour period. **2** the duration of daily exposure of an organism to illumination; the length of this period that favours optimum functioning. —**photoperiodic** *adj.*; **photoperiodically** *adv.*

photoperiodism *or* **photoperiodicity** the response of an organism to the relative durations of light and dark in a 24-hour period.

photophore any light-emitting organ of an animal.

photophosphorylation *or* **photosynthetic photophosphorylation** the metabolic processes by which photosynthetic organisms use light energy to convert ADP to ATP without the concomitant reduction of dioxygen to water that occurs in oxidative phosphorylation (*see* **photosynthesis**). There are two distinct electron transport mechanisms: in **noncyclic photophosphorylation**, which involves both photosystems I and II, ATP synthesis is linked to the transport of electrons from water to $NADP^+$, with production of NADPH and dioxygen; in **cyclic photophosphorylation**, which involves only photosystem I, ATP synthesis is driven by a proton gradient generated across the thylakoid membrane.

photopia adjustment of the eye to vision in light of moderate or high intensity, permitting perception of colour; it is considered to involve mainly the **cone cells** of the retina. *Compare* **scotopia**. —**photopic** *adj.*

photopigment any pigment whose chemical state depends on the intensity of the light falling on it.

photopolymerize *or* **photopolymerise** to effect polymerization by the action of light. —**photopolymerization** *or* **photopolymerisation** *n.*

(6–4)photoproduct a type of **pyrimidine dimer**.

photoprotein any protein actively concerned in the emission of light by a living organism.

photopsin an **opsin** that is the apoprotein of an **iodopsin**.

photoreactivating enzyme *see* **DNA photolyase**, **photoreactivation**.

photoreactivation the process by which genetic damage caused to organisms by ultraviolet radiation can be reversed by subsequent illumination with visible or near-ultraviolet light. The pyrimidine dimers formed in DNA by the action of ultraviolet light bind **DNA photolyase**, which absorbs light, maximally at 380 nm, and catalyses the restoration of two pyrimidine residues in the DNA.

photoreactive (of a substance or reagent) reactive in a photochemical reaction. —**photoreactivity** *n.*

photoreceptor any biological structure that responds to incident electromagnetic radiation, particularly visible light. It especially refers to a cell that, on absorbing light, generates a nerve impulse or impulses.

photoreduction **1** chemical reduction brought about by electromagnetic radiation, especially visible light. **2** a process occurring at low light intensities in certain algae whereby dihydrogen functions in place of water as an electron donor for the reduction of carbon dioxide and oxygen is not evolved; at higher light intensities normal photosynthesis takes place. **3** reduction in size photographically.

photorespiration a light-dependent catabolic process occurring concomitantly with photosynthesis in plants (especially **C_3 plants**) whereby dioxygen is consumed and carbon dioxide is evolved. The substrate is glycolate formed in large quantities in chloroplasts from 2-phosphoglycolate generated from ribulose 1,5-bisphosphate by the action of **ribulose-bisphosphate carboxylase**; the glycolate enters the peroxisomes where it is converted by **glycolate oxidase** to glyoxylate which undergoes transamination to glycine. This then passes into the mitochondria where it is decarboxylated. C_3 plants may lose 20–40% of photosynthetically fixed carbon by photorespiration, whereas **C_4 plants** lose relatively little. C_4 plants defeat photorespiration in two ways. First, they recapture released CO_2 in the cytoplasm using **phospho*enol*pyruvate carboxylase** which has a very high affinity for CO_2. Although this does not directly affect photorespiration, it prevents loss of CO_2. Second, they concentrate CO_2 near ribulose-biphosphate carboxylase, and this increases the CO_2:O_2 ratio, which has the effect of inhibiting the oxygenase activity. —**photorespiratory** *adj.*

photosensitivity **1** the property of being reactive or unusually reactive to incident photons, especially to those of visible light. **2** *(in medicine)* an abnormal, local or generalized reaction to sunlight, due to the accumulation in the skin of **photodynamic** substances, either endogenous or exogenous. —**photosensitive** *adj.*

photosensitize *or* **photosensitise** **1** to render photosensitive; *see* **photosensitivity**. **2** to render a target molecule more reactive (e.g. more easily oxidized) by the addition to it of a second type of molecule, often a dye, that absorbs light energy and transfers it to the target molecule. —**photosensitization** *or* **photosensitisation** *n.*

photosensitizer *or* **photosensitiser** any substance that photosensitizes or is photodynamic.

photosuicide inhibitor a type of **suicide inhibitor** that, after reaction with an enzyme or other appropriate protein, is capable of being selectively photodecomposed to a highly reactive species that can irreversibly modify the protein in the neighbourhood of its active site.

photosynthate any product of the dark reactions of photosynthesis.

photosynthesis **1** *(in biology)* the synthesis by organisms of organic chemical compounds, esp. carbohydrates, from carbon dioxide using energy obtained from light rather than from the oxidation of chemical compounds (*compare* **chemosynthesis**). In higher plants, green algae, and cyanobacteria, water is the electron donor and dioxygen is evolved; in other photosynthetic bacteria, however, various other simple substances (e.g. H_2S) may act as electron donors, dioxygen is not formed, and the photosynthetic pathway is simpler. Photosynthesis comprises two separate processes: the light reactions and the dark reactions of photosynthesis. The system in higher plants, green algae, and cyanobacteria brings about an overall reaction in which electrons are released from water molecules and are transferred through complexes of chlorophylls, cytochromes, proteins, and small molecules to $NADP^+$, reducing it to NADPH. Protons are released from water and form a chemiosmotic gradient that results in the formation of ATP by a process similar to that operating in mitochondria (*see* **chemiosmotic coupling hypothesis**). These are the **light reactions**. The NADPH and ATP formed by these reactions then drive the **dark reactions** i.e. the **reductive pentose phosphate cycle**. The electrons and protons are released from water by the oxygen-evolving complex (*abbr.*: OEC), and dioxygen is formed in the process. The sequence of reactions involves the OEC, from which electrons pass to photosystem II (*see* **photosystem**), thence to **plastoquinone** reducing it to a quinol which then reduces the cytochrome b_6–f complex. This in turn reduces **plastocyanin** which passes electrons to photosystem I (*see* **photosystem**) which then reduces $NADP^+$ to NADPH. In photosynthetic bacteria, a simpler system exists, in which water is not split, dioxygen is not evolved, and $NADP^+$ is not reduced directly. In this system, photons excite molecules of bacteriochlorophyll *b* in a **photosynthetic reaction centre** to transfer electrons through a cyclic electron-transfer system.

Cyclic electron flow can also occur under some conditions in plants, and involves only photosystem I, electrons being released by photon activation from photosystem I and returned to it through cytochrome b_6–f and plastocyanin, with pumping of protons to generate ATP. Under these conditions there is no reduction of $NADP^+$. **2** *(in chemistry)* any synthesis by a

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photochemical reaction. —**photosynthetic** *adj.*; **photosynthetically** *adv.*

photosynthetic phosphorylation *an alternative term for* **photophosphorylation**.

photosynthetic quotient a ratio of the rate of dioxygen evolution by a cell or organism capable of photosynthesis to that of carbon dioxide uptake. It is an index of photosynthetic activity relative to respiration (including photorespiration).

photosynthetic reaction centre the photosynthetic complex in bacteria, consisting essentially of a transmembrane protein of three subunits, denoted L, M, and H. Collectively the three subunits generate 11 transmembrane helices. Although the L and M helices (which have binding sites for the many prosthetic groups) are different, the groups themselves are arranged with near twofold symmetry because of similarities in the folds of the subunits. The L and M subunits bear bacteriochlorophyll, bacteriopheophytin, ubiquinone, and menaquinone molecules. The bacteriochlorophylls will be either *a* or *b* types, as will be the bacteriopheophytins. Here we describe a system with *b* types. Of the four bacteriochlorophyll *b* molecules, two constitute a 'special pair' with an Mg^{2+}–Mg^{2+} distance of 7 Å and in hydrophobic environments; other prosthetic groups are **bacteriopheophytin** *b* (two molecules), one nonheme Fe(II), one **ubiquinone**, and one **menaquinone**. There is cyclic electron flow through a cytochrome bc_1 complex, cytochrome *c*, and the bacteriochlorophyll–bacteriopheophytin complex, protons being pumped from the bacterial cytosol to the periplasmic space, and then returning to the cytosol through an ATP synthase with synthesis of ATP. The system differs from that in plants in that there is only one type of reaction centre, no splitting of water, and no direct reduction of $NADP^+$. Its essential features are that photons excite electrons in the 'special pair' and these excited electrons then flow through the bacteriochlorophyll–bacteriopheophytin complex, ubiquinone, and menaquinone, dissipating energy in bringing about protein pumping to form the chemiosmotic gradient that results in ATP formation. They then return to the 'special pair' via cytochromes bc_1 and *c*. Examples from *Rhodobacter sphaeroides*: L subunit: database code NRL_4RCRL, 266 amino acids (29.74 kDa); M subunit: database code NRL_4RCRM, 296 amino acids (33.15 kDa); H subunit: database code NRL_4RCRH, 237 amino acids (25.63 kDa). This (and the complex from *Rhodopseudomonas viridis*) represents the first transmembrane protein to have its 3-D structure determined in atomic detail by X-ray crystallography (by Deisenhofer, **Michel**, and **Huber**). *See also* **P870**, **P960**, **photosystem** (def. 2).

photosystem **1** either of the two functionally distinct but cooperating systems, designated photosystem I (*abbr.*: PSI) and photosystem II (*abbr.*: PSII), between which are distributed the various molecules that effect the light reactions of **photosynthesis**; photosystems are located in the **thylakoid** membranes of the chloroplasts of higher plants and green algae or in the free thylakoid membranes of cyanobacteria. Photosystem I consists of a transmembrane multisubunit complex, of about 10 subunits in all, consisting of a heterodimer complex of PsaA and PsaB which binds P700, together with the chlorophyll acceptor A_0, the phylloquinone acceptor A_1, and Fx, a 4Fe–4S centre. PsaC, which is bound to this complex, contains two additional 4Fe–4S centres required for ferredoxin reduction. Other subunits are involved in binding soluble ferredoxin, ferredoxin-NADP oxidoreductase and regulation of electron flow. Approximately 100 chlorophyll *a* molecules are bound to the minimal heterodimer unit. Examples (all from pea), heterodimer of two similar subunits, A_1: database code PSAA_PEA, 761 amino acids (84.01 kDa) and A_2: database code PSAB_PEA, 734 amino acids (83.32 kDa); PsaC: database code PSAC_PEA, 80 amino acids (8.84 kDa) is similar to bacterial-type 4Fe–4S **ferredoxins**. Photosystem II is formed from a heterodimer of the D_1 and D_2 proteins which bind P680, together with the pheophytin acceptor, two plastoquinone acceptors Q_a and Q_b, and a non-heme iron atom. The minimal purified unit contains about six chlorophyll *a* molecules. **Cytochrome b_{559}** is always associated with PSII. A large number of other subunits including light-harvesting chlorophyll-protein complexes, proteins involved in stabilizing the Mn complex, and regulatory subunits are required to form a functional photosystem II. Examples (from pea) of proteins of photosystem II are D_1 precursor: database code PSBA_PEA, 353 amino acids (38.92 kDa); and D_2 precursor: database code PSBC_PEA, 353 amino acids (39.51 kDa). **2** any functionally analogous but simpler single photosystem present in photosynthetic bacteria. That from *Rhodopseudomonas viridis* contains three hydrophobic subunits, a special pair of bacteriochlorophyll *b* (the reaction-centre bacteriochlorophyll P960), two molecules of bacteriopheophytin *b* (*see* **bacteriopheophytin**), a bound iron atom and one molecule each of **ubiquinone** and a **menaquinone**. There are four heme *c*-type cytochromes in this case (but not in all). The complete structure has been determined by X-ray crystallography. *See also* **photosynthetic reaction centre**.

phototaxis the movement of a motile cell or organism towards (**positive phototaxis**) or away from (**negative phototaxis**) a source of light. —**phototactic** *adj.*

phototoxic able to cause physiological damage by making the skin abnormally sensitive to light. —**phototoxicity** *n.*

phototransistor a type of junction transistor that responds to incident light or other electromagnetic radiation by the generation of an electric current, which is then amplified.

phototroph *or* **phototrophe** any organism whose principal or only source of primary energy is sunlight. The great majority of such organisms are **photoautotrophs** (*or* **photolithotrophs**), which use light energy to synthesize their organic requirements solely from inorganic precursors; these include all green plants and algae, cyanobacteria, and green and purple sulfur bacteria. Relatively few phototrophs are **photoheterotrophs** (*or* **photoorganotrophs**), which require a supply of organic precursors to manufacture their own organic components; examples include certain purple nonsulfur bacteria. *Compare* **chemotroph**. —**phototrophic** *adj.*; **phototrophy** *n.*

phototropic **1** involving or showing **phototropism**. **2** involving or showing phototropy (i.e. **photochromism**).

phototropism the orientation or growth of a cell or (a part of) an organism in relation to a source of light. The term is used especially of plants or plant organs.

phototropy *an alternative term for* **photochromism**.

phototube a type of photocell consisting of a vacuum tube or gas-filled tube in which a photocathode responds to incident light or other electromagnetic radiation by emission of electrons.

pH paper absorbent paper, usually in strip form, that is impregnated with a colour-changing pH indicator dye. It is useful for estimating the approximate pH of a solution.

pH profile *see* **pH-activity profile**.

phragmoplast a structure formed in the developing plant cell wall from the endoplasmic reticulum and spindle fibres. It is observed during **cytokinesis** in plant cells as a cylindrical structure, composed of microtubules, between the two sets of daughter chromosomes. The microtubules are those of the two sets of polar microtubules of the **spindle**. These microtubules transport small Golgi-derived vesicles to the equatorial (or central) region, which fuse there to form the early **cell plate**, which then grows out to join up with the cell wall.

phrenosin a **cerebroside** in which the acyl constituent is cerebronate. *See* **lignocerate**, of which cerebronate is the 2-hydroxy derivative.

pH standard any of a set of six standard solutions which may be used as primary pH standards; they are: potassium hydrogen tartrate, saturated at 25 °C, pH 3.557 at 25 °C; 0.1 mol/kg potassium dihydrogen citrate, pH 3.776 at 25 °C; 0.025 mol/kg KH_2PO_4 + 0.025 mol/kg Na_2HPO_4, pH 6.865 at 25 °C;

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0.008695 mol/kg KH_2PO_4 + 0.03043 mol/kg Na_2HPO_4, pH 7.413 at 25 °C; 0.01 mol/kg disodium tetraborate, pH 9.180 at 25 °C; 0.025 mol/kg $NaHCO_3$ + 0.025 mol/kg Na_2CO_3, pH 10.012 at 24 °C.

pH-stat an instrument for maintaining a constant pH in an aqueous liquid mixture in which hydrogen ions are being liberated or taken up. It is frequently arranged to measure the amount of reagent, as a function of time, that has to be added to maintain a predetermined pH.

Pht< *or* **–Pht–** *symbol for* the (divalent) phthaloyl group.

Pht– *symbol for* the (univalent) phthalyl group.

phthalate **1** *the trivial name for* 1,2-benzene dicarboxylate, the dianion of phthalic acid. **2** any mixture of phthalic acid and its mono- and dianions. **3** any salt or ester of phthalic acid.

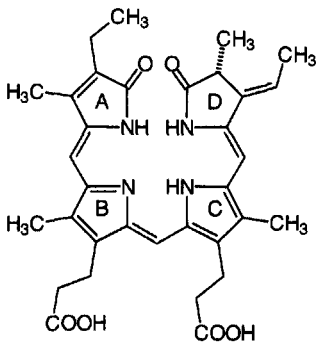
phthaloyl *symbol*: Pht< *or* –Pht–; the divalent acyl group, –OC–C_6H_4–CO–, derived from phthalic acid.

phthalyl *symbol*: Pht–; the univalent acyl group, HOOC–C_6H_4–CO–, derived from phthalic acid.

pH unit the difference between any two successive integral values of pH.

phyco+ *comb. form* denoting seaweed or other algae.

phycobilin any **bilin** found in **phycobiliproteins**. The two most common are **phycocyanobilin** and **phycoerythrobilin**. They are linear tetrapyrroles or **open tetrapyrroles**, i.e. chains of four pyrroles, the terminal pyrroles not being linked to each other to form the cyclic tetrapyrrole structure. The structure of phycocyanobilin is shown; phycoerythrobilin is similar except that the ethyl group on ring A is –CH=CH_2 and the methyne group between rings A and B is a methylene group.



phycocyanobilin

phycobiliprotein *or* **biliprotein** any phycobilin–protein conjugate found in the algae of the phyla Cryptophyta and Rhodophyta, and in cyanobacteria. Phycobiliproteins are intensely coloured and fluorescent water-soluble globular proteins. The two most common types, **phycocyanin** and **phycoerythrin**, are composed of two kinds of subunits, α (10–20 kDa) and β (14–30 kDa), each of which carries about three molecules of covalently bound **phycobilin** (phycocyanobilin in phycocyanin, phycoerythrobilin in phycoerythrin) and is present *in vivo* most commonly as aggregates of formula $(\alpha,\beta)_n$ where *n* is 3 or 6. Phycocyanin (blue: A_{max} at 618 nm) predominates in Cyanophyta, and phycoerythrin (red: A_{max} at 545 nm) predominates in Rhodophyta. A third type, **allophycocyanin** (pale blue: A_{max} at 650 nm), present in small amounts in both Cyanophyta and Rhodophyta, has only one type of protein subunit (≈15.5 kDa), carries one molecule of covalently bound phycocyanobilin, and is present *in vivo* as aggregates of six subunits. It is a heterodimer of α and β chains. Example from *Mastigocladus laminosus* (β chain only available): database code PHBB_MASLA, 169 amino acids (18.84 kDa). *See also* **phycobilisome**.

phycobilisome any of the granules, approximately 32 nm × 48 nm and consisting of highly aggregated **phycobiliproteins**, that are attached in arrays to the external face of a **thylakoid** membrane in algae of the phyla Cyanophyta and Rhodophyta, where they function as light-harvesting devices in photosynthesis. Excitation energy in the phycobilisome flows in the sequence:

phycoerythrin → phycocyanin → allophycocyanin,

whence it passes to the antenna chlorophyll of photosystem II. In Cyanophyta it is also known as a **cyanosome**.

phycocyanin a blue phycobilin; *see* **phycobiliprotein**.

phycocyanobilin a type of **phycobilin**; *see also* **phycobiliprotein**.

phycoerythrin a red phycobilin; *see* **phycobiliprotein**.

phycoerythrobilin a type of **phycobilin**; *see also* **phycobiliprotein**.

phycofluor any artificial conjugate of a **phycobiliprotein** with a molecule conferring biological specificity (e.g. avidin, immunoglobulin, protein A). Such conjugates are useful in fluorescence immunoassay and fluorescence-activated cell sorting by virtue of the distinctive and intense fluorescence of the phycobiliprotein moiety.

phycotoxin any poisonous substance produced by algae.

phyl+ *a variant form of* **phylo+** (sometimes before a vowel).

phyla the plural of **phylum**.

PHYLIP a suite of computer programs used for determining phylogeny and/or cladistic relationships from protein and/or nucleic-acid sequences, using, in part, **parsimony**.

phyllo+ *or (before a vowel)* **phyll+** *comb. form* denoting leaf.

phyllocerulein *or (esp. Brit.)* **phyllocaerulein** *see* **cerulein**.

phylloquinone *abbr.*: K; *the recommended name for* vitamin K_1; 2-methyl-3-phytyl-1,4-naphthoquinone. *See* **vitamin K**.

phylo+ *or (sometimes before a vowel)* **phyl+** *comb. form* denoting race or tribe.

phylogenetic tree a graphical representation of the (putative) evolutionary relationships of a group of organisms.

phylogeny the evolutionary history of an organism or group of related organisms. In biochemistry, such evolutionary relationships are based on similarities and differences in nucleic acid or protein sequences. —**phylogenetic** *or* **phylogenic** *adj.*

phylum (*pl.* **phyla**) a primary taxon of animals or plants (in plants also termed division). It consists of a number of classes (or sometimes a single class).

physalaemin Glp-Ala-Asp-Pro-Asn-Lys-Phe-Tyr-Gly-Leu-Met-NH_2; an 11-residue peptide amide **tachykinin** from the skin of the amphibian *Physalaemus fuscumaculatus*. It is more potent than **eledoisin** and **substance P** in some assay systems, and is useful in the study of receptors for substance P.

physeteric acid *see* **tetradecenoic acid**.

physical **1** of, or pertaining to, matter and energy; of material things. **2** of, or relating to, natural science, especially of non-living systems. *Compare* **biological**. **3** having reference to or used in physics. —**physically** *adv.*

physical adsorption *an alternative term for* **physisorption**.

physical biochemistry the application of physical chemistry to biochemical substances, structures, and systems. Often used synonymously with **biophysical chemistry**.

physical chemistry the branch of chemistry concerned with the relationship between the physical properties of substances and their chemical properties, reactions, and structures.

physical map a map which identifies the physical location of genes on a chromosome in contrast to a **linkage map** which is generated by measuring recombination frequencies. Physical length may be measured in base pairs, kilobases, or megabases. Such maps are obtained, e.g. in **pulsed field gel electrophoresis**, **fluorescence *in situ* hybridization**, and **contig** mapping.

physico+ *comb. form* denoting physical or of physics.

physicochemical of, pertaining to, or using the methods of physical chemistry. —**physicochemically** *adv.*

physics *functioning as sing.* the branch of science concerned

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with the properties of matter and of energy, and with the interactions and interconversions between matter and energy.

physiological 1 of, pertaining to, or used in physiology. **2 normal** (def. 4); not **pathological** (def. 2) or **pharmacological** (def. 2). —**physiologically** *adv.*

physiological antagonist a drug that produces the opposite effect to a specified agonist by an action that is unrelated to that of the agonist.

physiological chemistry *an older term for* **biochemistry** (especially that of humans and higher animals).

physiological conditions *environmental conditions simulating those under which the (normal) functions of a cell, organ, or tissue can be expressed.*

physiological saline *or (sometimes)* **normal saline** a (sterile) solution of 0.9% w/v (0.154 mol L^{-1}) sodium chloride in water. It is approximately isotonic with mammalian blood and lymph, and is useful in the temporary maintenance of living cells and tissues, and as a vehicle for injections.

physiology the science dealing with the functioning of cells, tissues, organs, and organisms, and with the chemical and physical phenomena concerned.

physisorption *or* **physical adsorption** *or* **van der Waals adsorption** the type of **adsorption** (def. 1) in which only van der Waals forces are involved and hence in which no significant changes occur in the electronic orbital patterns of the interacting substances. *Compare* **chemisorption**.

physostigmine *or* **eserine** a toxic alkaloid extracted from Calabar beans (*Physostigma venenosum*). It inhibits **cholinesterase** by binding to the anionic site of the enzyme, forming a carbamoyl ester of the serine hydroxyl, which is only slowly hydrolysed. It has been used in West Africa in witch ordeals.

phyt+ *a variant form of* **phyto+** (before a vowel).

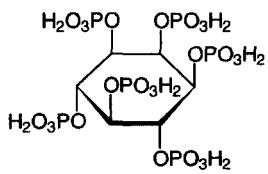
phytanic acid 3,7,11,15-tetramethylhexadecoanoic acid; a branched chain fatty acid that is formed metabolically from **phytol**, a constituent of chlorophyll, by bacteria in the ruminant stomach. Its oxidation in animals depends on the **alpha oxidation** pathway, since the methyl group on C-3 (the beta carbon) blocks beta oxidation. After alpha oxidation this methyl group is on C-2 of the product, so that beta oxidation can occur, releasing propionyl-CoA as a product..

phytase either of the two enzymes, designated 3-phytase (EC 3.1.3.8) and 6-phytase (EC 3.1.3.26), that catalyse the hydrolytic removal of a phosphoric residue from **phytate** at the 3-position or the 6-position, respectively; most commonly it signifies 6-phytase.

phytate any anion of **phytic acid**, any mixture of free phytic acid and its ionized forms, or any salt of phytic acid. It is the major phosphorus compound in plants and is important for phosphate storage in cereal grains, especially as its calcium–magnesium salt, **phytin**. In higher animals phytin binds dietary Ca^{2+} and Mg^{2+}, making them less available.

+phyte *noun suffix* denoting **1** plant (of the habitat or type specified). **2** pathological outgrowth. —**+phytic** *adj.*

phytic acid *the trivial name for myo*-inositol hexakis(dihydrogen phosphate). *See* **phytate**.



phytin *see* **phytate**.

phyto+ *or (before a vowel)* **phyt+** *comb. form* denoting plant.

phytoagglutinin *or (rarely)* **phytohemagglutinin** any plant **lectin**. The majority are glycoproteins, although some, e.g. **concanavalin A**, contain no carbohydrate. They accumulate mainly in seeds, in cytoplasm of cotyledons and embryonic cells, although they are synthesized in leaves.

phytoalexin any substance with antibiotic activity that is produced by plant tissues in response to infection, especially with a fungus. A variety of different types of substance are regarded as phytoalexins. They include compounds as divergent as ***phaseollin***, *some sesquiterpenes and long-chain acetylenic* alcohols.

phytochelatin any of a group of peptides that bind heavy metals (Cd, Zn, Cu, Pb, Hg) in thiolate coordination complexes, and can be isolated from plant cell suspension cultures. The structure is of the type $(\gamma$-glutamyl-cysteinyl$)_n$-glycine, where n is 2 to 11.

phytochemistry the branch of chemistry concerned with plants, especially with **secondary metabolites**.

phytochrome a chromoprotein present in trace amounts in all higher plants and involved in regulating light-dependent processes such as leaf development and flowering. It consists of a **phycobilin**-related chromophore covalently linked to a polypeptide of ≈124 kDa. Phytochrome exists in two forms, P_R (A_{max} at 666 nm) and P_{FR} (A_{max} at 730 nm), which are indefinitely interconvertible on absorption of light in the red and far-red regions of the spectrum, respectively. The spectral changes are due to *cis–trans* isomerization in the phycobilin. The active form, P_{FR}, plays a central role in light-promoted modulation of gene expression, which is of importance in plant growth and development in every phase of the life cycle; conversion of P_{FR} to P_R cancels these responses. The phytochromes are homodimeric proteins with a linear tetrapyrrole chromophore covalently linked to a polypeptide. Examples, phytochrome A (vegetable marrow): database code PHYA_CUCPE, 1124 amino acids (124.94 kDa); phytochrome B (tobacco): database code PHYB_TOBAC, 1132 amino acids (125.67 kDa).

phytoecdysone *(sometimes)* any member of the group of **ecdysteroids** found in plants.

phytoglycogen plant glycogen; a highly branched polymer of D-glucose, with a structure similar to that of animal **glycogen**, found in fungi, corn (maize), and rice. A similar substance is found in bacteria and cyanobacteria. In contrast to the major branched chain glucan, amylopectin, which is found only as a component of starch, plant glycogen is found as an independent molecule.

phytohemagglutinin *or (esp. Brit.)* **phytohaemagglutinin** **1** *abbr.*: PHA; *or* **phytomitogen** the **lectin** from the red kidney bean, *Phaseolus vulgaris*; a potent mitogen. Example, leukoagglutinating phytohemagglutinin precursor: database code PHAL_PHAVU, 272 amino acids (29.56 kDa). **2** *a rare alternative name for* **phytoagglutinin**.

phytohormone *or* **plant hormone** any plant growth factor or similar substance that regulates plant development. The group is diverse and includes **abscisic acid**, **auxins**, **ethylene**, **cytokinins**, and **gibberellins**.

phytokinin *an alternative term for* **cytokinin**.

phytol *a trivial name for trans-* (or *E*-) (7*R*,11*R*)-3,7,11,15-tetramethyl-2-hexadecen-1-ol; the pure substance is a colourless oily liquid. Phytol occurs in combined form in chlorophyll and vitamin K_1. *See also* **phytyl**.

phytolysosome a **lysosome** of plant cells.

phytomitogen *an alternative name for* **phytohemagglutinin** (def. 1).

phytoplankton plant plankton; consisting of diatoms, dinoflagellates, and other microscopic algae.

phytoporphyrin any plant **porphyrin**.

phytosphingosine 2*S*,3*S*,4*R*-2-amino-1,3,4-octadecanetriol; a constituent of many plant sphingolipids.

phytosterol any sterol occurring in higher plants; they differ from animal sterols in having C_1 or C_2 residues at C-24 and/or a double bond at C-22.

phytotoxic toxic to a plant.

phytotoxin **1** any toxin produced by a plant. **2** any substance that is toxic to a plant or plants.

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phytotron a laboratory where plants can be grown and studied under a variety of controlled conditions.

phytyl the alkyl group, $(CH_3)_2$–CH–$[CH_2]_3$–CH(CH_3)–$[CH_2]_3$–CH(CH_3)–$[CH_2]_3$–C(CH_3)=CH–CH_2–, (*E*)-(7*R*,11*R*)-3,7,11,15-tetramethyl-2-hexadecenyl, derived from **phytol**.

pi **1** *symbol*: π (lower case) *or* Π (upper case); the sixteenth letter of the Greek alphabet. For uses *see* **Appendix A**. **2** *(in mathematics) symbol*: π; a transcendental number that is the ratio of the circumference of a circle to its diameter. It has the approximate value 3.141 592 653 59.

pI *symbol for* isoelectric point.

PI *abbr. for* phosphatidylinositol.

pi adduct *or* **π adduct** any adduct formed by coordination and involving donation of an electron pair from a **pi orbital** into a **sigma orbital**, from a sigma orbital into a pi orbital, or from a pi orbital into a pi orbital. It is also known, less correctly, as a **pi complex**.

pi bond *or* **π bond** the type of covalent bond formed between atoms by electrons occupying a **pi orbital**.

picein (wax) an unreactive thermoplastic material, composed of a mixture of hydrocarbons of very low vapour pressure, that adheres well to glass and metal. It is useful as a sealing substance in the assembly of vacuum systems.

Pichia *see* **methylotrophic yeasts**.

picket-fence (porphyrin) complex any synthetic iron–porphyrin complex in which the porphyrin has been derivatized with four large groups attached to one side of the porphyrin ring, to each of the inter-pyrrole carbon atoms, so as to form a protective enclosure for the binding of a dioxygen molecule as in **myoglobin** or **hemoglobin**.

pico- *symbol*: p; SI prefix denoting 10^{-12} times.

picogram *symbol*: pg; a unit of mass equal to 10^{-15} kilogram or 10^{-12} gram.

picometre *or (US)* **picometer** *symbol*: pm; a unit of length equal to 10^{-12} metre.

picomolar *symbol*: pM *or* pM; describing a solution containing one picomole of solute per litre of solution, or a specified multiple or fraction thereof; used also of a substance concentration similarly expressed.

picomole *symbol*: pmol; a unit of amount of substance equal to 10^{-12} mole.

pi complex *or* **π complex** *a less suitable name for* **pi adduct**.

picoplankton plankton having cell dimensions of between 0.2 and 2 μm and including bacteria, cyanobacteria, some algae, and certain microscopic protozoans. Picoplankton appears to be ubiquitous in open waters of lakes and seas and probably exceeds in total biomass any other group of pelagic organisms.

picornavirus any of a group of RNA animal viruses consisting of naked, icosahedral 27 nm capsids with single-stranded infectious RNA (plus strand) of 2.7 MDa. The group includes human poliovirus, some common-cold viruses, and foot-and-mouth disease virus (of cattle and other cloven-footed mammals).

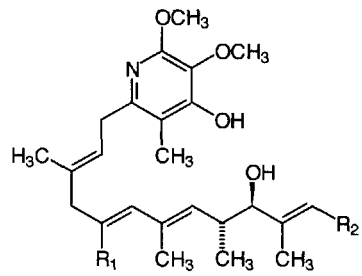
picosecond *symbol*: ps; a unit of time equal to 10^{-12} second.

4-pi counter any type of radiation counter that detects radiation emitted through a solid angle of 4π steradians, i.e. in all directions from a source.

picrotoxin *or* **cocculin** a preparation containing an equimolar mixture of **picrotoxinin** ($C_{15}H_{16}O_6$) and **picrotin** ($C_{15}H_{18}O_7$) obtained from the seeds of *Anamirta cocculus* (fishberries). It contains a potent ligand for the chloride ionophore of the $GABA_A$ receptor, binding to the channel protein and inhibiting Cl^- transport without displacing GABA; this endows it with potent convulsant activity. It can thus also act as an antidote to barbiturates, which enhance GABA binding. It is displaced from its binding site by anticonvulsants.

pi electron *or* **π electron** an electron in a **pi orbital**.

piericidin A an antibiotic that is a structural analogue of **ubiquinone**. It is a classical inhibitor of mitochondrial electron transport similar in action to **rotenone**. It is a potent inhibitor of NADH:ubiquinone oxidoreductase (*see* **NADH dehydrogenase**), acting at or near the ubiquinone catalytic site.



pig **1** any nonruminant, omnivorous ungulate mammal of the family Suidae, especially the domestic pig, *Sus scrofa*. **2** *informal* short for **guinea pig**.

PI-G *abbr. for* phosphatidylinositolglycan.

PIG-A *abbr. for* phosphatidylinositol glycan protein class A.

pigeon any stout-bodied bird of the family Columbidae, especially the domesticated or feral pigeon, *Columba livia*. Pigeon-breast muscle has been extensively used as a convenient tissue for the study of oxidative metabolism.

pigment **1** any general or particular colouring matter in living organisms. **2** any natural or artificial substance used to impart colour. **3** to colour with pigment.

pigment 680 *see* **P680**.

pigment 700 *see* **P700**.

pigmentation **1** natural coloration of organisms. **2** an increase in such coloration.

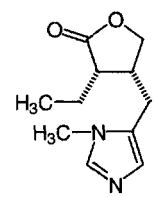
pigment system *an alternative name for* **photosystem**.

PI-G-tailed proteins proteins that are anchored to the membrane through linkage to phosphatidylinositol-glycan.

pili the plural of **pilus**.

pilin any protein subunit of a bacterial **pilus**.

pilocarpine an alkaloid extracted from *Pilocarpus jaborandi*; it has muscarinic cholinomimetic activity.



pilot plant a prototype apparatus set up to develop and scale up a new manufacturing process.

pilus (*pl.* **pili**) a hairlike appendage, about 25 nm in diameter and 10–12 μm long, present sometimes on cells of certain Gram-negative bacteria, especially members of the Enterobacteriaceae and *Pseudomonas* spp., in addition to any flagella. The two main types, distinguishable morphologically and antigenically, are **common pilus** and **sex pilus**, both of which may be present on the same cell. Up to several hundred common pili per cell may be present, either distributed over the entire surface or concentrated at a pole; their function is not known. Only one or two sex pili commonly are present; they appear to be required for bacterial **conjugation**. Both types of pili are thought to be tubes or tubelike structures formed from one or two helically wound strands, each of which consists of a linear arrangement of molecules of the protein pilin. The term pilus is often used interchangeably with **fimbria**, but may be used specifically to mean sex pilus (in which case fimbria then denotes common pilus).

PIM a gene family encoding serine/threonine kinases of un-

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known function named from proviral integration site MuLV-induced murine T-cell lymphomas. They are highly conserved between human and mouse, and are expressed at high levels in hemopoietic tissues, testes and ovaries, and embryonic stem cells. Example of gene product from mouse: database code KPIM_MOUSE, 313 amino acids (35.54 kDa).

pI marker an **isoelectric point marker**; *see* **isoelectric point**.

pineal body *or* **pineal gland** a small, pine-cone-shaped structure situated deep between the cerebral hemispheres of the mammalian brain. It elaborates and secretes **melatonin**.

pineal hormone *an older name for* **melatonin**.

ping-pong mechanism *an alternative name for* **double-displacement (enzyme) mechanism**.

pinocytic *an alternative term for* pinocytotic (*see* **pinocytosis**).

pinocytic vesicle *an alternative term for* **pinocytotic vesicle**.

pinocytosis the process whereby cells take in liquid material from their external environment; literally 'cell drinking'. Liquid is enclosed in vesicles, formed by invagination of the plasma membrane. These vesicles then move into the cell and pass their contents to endosomes. Pinocytosis is the type of **endocytosis** occurring in most types of cells; hence the term is often applied interchangeably with endocytosis to such cells (*compare* **phagocytosis**). —**pinocytotic** *or* **pinocytic** *adj.*

pinocytotic vesicle *or* **pinocytic vesicle** a cellular vesicle serving **pinocytosis**; an alternative term to **endocytotic vesicle** when containing nonparticulate material.

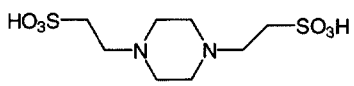
pinosome *an alternative name for* **endosome** (def. 1) (when containing nonparticulate material).

pi orbital *or* **π orbital** a bonding molecular orbital formed by the in-phase, sideways-on overlap of parallel p atomic orbitals, one from each of two atoms, to produce a charge-density distribution that is mainly between the atomic nuclei but maximal in two zones, one on either side of and parallel to the internuclear axis. When occupied by two electrons of opposed spins it becomes the second bond in a double covalent bond (two such occupied orbitals, mutually orthogonal, providing the second and third bonds of a triple bond).

PIP *or* **PI 4-P** *abbr. for* phosphatidylinositol 4-phosphate.

PIP_2 *or* **PI 4,5-P_2** *abbr. for* phosphatidylinositol 4,5-bisphosphate.

Pipes *or* **PIPES** *abbr. for* 1,4-piperazinediethanesulfonic acid; a **Good buffer substance**; pK_a (20 °C) = 6.8.



pipette *or (US)* **pipet** **1** any device for transferring or delivering (usually measured) volumes of liquid and commonly consisting of a slender, calibrated glass or plastic tube with a finely drawn-out delivery tip and (for larger volumes) a centrally placed bulb. It may be filled by applied suction or by capillarity (according to its bore), and emptied by drainage or by applied pressure. **2** to transfer or deliver a (usually measured) volume of liquid with a **pipette** (def. 1). —**pipettable** *adj.*

pipettor any device for the rapid, repetitive dispensing of a predetermined volume of a liquid.

pipsyl *symbol*: Ips; *p*-iodophenylsulfonyl; I-C_6H_4-SO_2; a chemical group with which free amino groups may be derivatized by reaction with pipsyl chloride, *p*-iodophenylsulfonyl chloride. *Compare* **tosyl**.

pipsylate to convert (an amino compound) to a **pipsyl** derivative. —**pipsylation** *n.*

Pirani gauge an electric gauge for low gas pressures that functions over the range 10^{-2} to 10^{-5} mm Hg. It depends on the principle that an electrically heated wire loses heat by conductivity, and thus varies in electric resistance, to an extent empirically dependent on the pressure of the surrounding gas.

piscine of, relating to, or being a fish.

pitch height (of a helix) *symbol*: *p*; the linear displacement along the axis of a helix corresponding to one complete turn of the helix.

PIT a gene encoding the pituitary-specific positive transcription factors, Pit. It activates the genes for somatotropin and prolactin, binding specifically to the consensus sequence 5′-TAAAT-3′. It contains a **POU domain** and contributes to the naming of the domain. Example Pit-1 from human: database code HMP1_HUMAN, 291 amino acids (32.91 kDa).

Pitocin *a proprietary name for* (a solution of) **oxytocin**.

Pitressin *a proprietary name for* (a solution of) **vasopressin**.

pituitary **1** pertaining to or produced by the **pituitary gland**. **2** the pituitary gland.

pituitary function *see* **combined test of pituitary function**.

pituitary gland *or* **hypophysis (cerebri)** the most important endocrine gland of vertebrates. It is situated below the brain, to which it is attached by a stalk, and measures about 8 mm by 12 mm in an adult human. It consists of two parts: the anterior lobe, or **adenohypophysis**, and the posterior lobe, or **neurohypophysis**; both lobes secrete a range of hormones.

Pituitrin *a proprietary name for* an aqueous extract of bovine neurohypophysis; it contains both oxytocin and vasopressin.

PIVKA *abbr. for* protein induced by vitamin K absence; examples of such substances are the abnormal proteins produced in vitamin K-deficient animals, corresponding to coagulation factors II, VII, IX, and X (*see* **blood coagulation**) in which some glutamate residues have not been carboxylated to γ-carboxyglutamate residues.

pixel one of the very small units that make up the image on a cathode-ray tube. [From 'pix' (i.e. pictures) + el(ement).]

p*K* *symbol for* the decadic logarithm of the reciprocal of a (thermodynamic) dissociation constant, *K*; i.e.

$$pK = \log 1/K = -\log_{10}K.$$

The type of constant may be indicated by a subscript: e.g. pK_a, a dissociation constant of an acid; pK_b, a dissociation constant of a base; pK_2, a second dissociation constant. For the dissociation of an acid, HA, to its ions, H^+ and A^-,

$$K = [H^+][A^-]/[HA].$$

Thus when $[A^-] = [HA]$, i.e. when the acid is half-dissociated, $K = [H^+]$, and hence p*K* is then equal to pH. Formerly symbolized as p_K. *See also* **group p*K***, **Henderson–Hasselbalch equation**, **molecular p*K***, **titration p*K***.

p*K′* *symbol for* the decadic logarithm of the reciprocal of an apparent (concentration) dissociation constant, *K′*.

pK_2 *see* **p*K***.

pK_a *see* **p*K***.

pK_b *see* **p*K***.

pK_w *symbol for* the decadic logarithm of the reciprocal of the ion product of water, K_w.

PK *(in clinical chemistry) abbr. for* pyruvate kinase.

PKC *abbr. for* protein kinase C.

PKU *abbr. for* phenylketonuria.

PL *abbr. for* **1** placental lactogen (i.e. **choriomammotropin**). **2** pyridoxal.

placebo (*pl.* **placebos** *or* **placeboes**) a tablet, capsule, or liquid medicine devoid of any specific pharmacological activity, but appearing identical to a preparation containing a biologically active substance. Placebos are used in human medicine for their psychological effects, and as controls in experimental therapeutics for elucidating the clinical actions of a drug.

placenta (*pl.* **placentas** *or* **placentae**) a highly vascularized organ within the uterus of a pregnant animal by which the embryo is attached to the uterine wall and through which the embryo can exchange solutes with the maternal circulation. The placenta also functions as an endocrine gland, secreting *inter alia* **choriogonadotropin**, **choriomammotropin**, and certain steroid hormones. —**placental** *adj.*

placental lactogen *abbr.*: PL; *an alternative name for* **choriomammotropin**.

plakoglobin *or* **desmoplakin III** a protein of **cell junctions**. It is

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thought to play a central role in the function of desmosomes and intermediate junctions. Example from human: database PLAK_HUMAN, 743 amino acids (81.40 kDa).

planar 1 of, or pertaining to, a **plane**. 2 lying in one plane; flat.

planchet *or* **planchette** a small, shallow dish used to contain a specimen for determination of its radioactivity with an end-window or windowless counter.

Planck, Max Karl Ernst Ludwig (1858–1947), German physicist; Nobel Laureate in Physics (1918) 'in recognition of the services he rendered to the advancement of Physics by his discovery of energy quanta'.

Planck constant *symbol*: h; a fundamental constant of proportionality between the frequency, ν, of electromagnetic radiation and the energy, E, of a quantum of the radiation; i.e. $h = E/\nu$. It has a value of $6.626\ 075\ 5(40) \times 10^{-34}$ J s.

plane 1 a surface in which a straight line joining any two contained points lies entirely within the surface; a flat surface. 2 an imaginary surface of such a kind within a real structure or lying conceptually in space. 3 lying wholly in one plane; flat or level; planar.

plane of polarization *or* **plane of polarisation** (of linearly **polarized light** or other electromagnetic radiation) the plane containing the electric vectors of the vibrations.

plane of symmetry a plane through a three-dimensional structure, e.g. a crystal or molecule, that divides the object into two parts that are mirror images of each other.

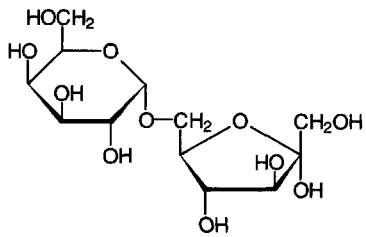
plane-polarized *or* **plane-polarised** *an alternative term for* **linearly polarized**. *See* **polarized light**.

planimeter a mechanical integrating instrument for measuring the area of an irregular plane figure. It consists of a moveable tracing arm, which is made to follow the boundary of the figure, and a dial on which the arm's motion is recorded. —**planimetry** *n*.

plankton *the collective term for* the small or microscopic plants (**phytoplankton**) and animals (**zooplankton**), that drift freely in the surface waters of lakes, seas, and oceans.

plant any organism of the kingdom Plantae. Plants are characterized by their ability to effect photosynthesis and the possession of rigid cell walls that contain cellulose.

planteobiose the disaccharide, 6-*O*-α-D-galactopyranosyl-D-fructose; a unit of the trisaccharide **planteose**.



α-anomer

planteose *O*-α-D-galactopyranosyl-(1→6)-*O*-β-D-fructofuranosyl-(2→1)-α-D-glucopyranoside; a trisaccharide isolated from defatted seeds of *Plantago ovata*.

plant hormone *an alternative term for* **phytohormone**.

plantibody a human antibody produced by genetically engineered tobacco plants.

plaque 1 any small disk-like object, patch, or zone. 2 a macroscopic or microscopic rounded clear zone in a layer of cells or bacterial lawn that results from the killing or lysis of adjacent cells by the action of a virus or other agent. 3 **a** (a patch of) fibrous or lipid material on the inner surface of an artery. **b** an area of tissue degeneration with distinctive histological features characteristic of certain (especially neurological) diseases, e.g. **kuru**, **multiple sclerosis**. 4 (a patch of) deposit closely adherent to the surface of a tooth that contains a mixed microbial flora and is composed largely of extracellular bacterial polysaccharide.

plaque-lift a technique used in recombinant DNA technology for screening actively expressing clones. Candidate clones for expression of a particular protein are plated out onto a dish. After incubation a nitrocellulose (or other) membrane is pressed against the surface of the plate, thereby adsorbing any protein 'plaques' formed by actively expressing clones. The membrane can then be screened, and the active clones identified.

+plasia *or* **+plasy** *comb. form* indicating development or growth. —**+plastic** *adj.*

plasm+ *a variant form of* **plasmo+** (before a vowel).

+plasm *comb. form* denoting the colloidal material of which living cells are composed. —**+plasmic** *adj.*

plasma 1 the proteinaceous fluid in which the cells of blood or lymph are suspended; the meaning is sometimes extended to include also the analogous fluid in which the fat droplets of milk are suspended. *See also* **blood plasma**. 2 *a less common word for* **protoplasm**. 3 *(in physics)* any region of highly ionized gas (as in a gas-discharge tube, a hot flame, or a thermonuclear reaction) containing approximately equal numbers of electrons and positively charged ions. It differs from ordinary gas in being a good conductor of electricity and being affected by a magnetic field. —**plasmatic** *or* **plasmic** *adj.*

plasma albumin *an alternative name for* **serum albumin**.

plasma cell *or* **plasmacyte** *or* **plasmocyte** a fully mature antibody-secreting B lymphocyte, found in lymphoid tissue and in connective tissue liable to encounter foreign material. It has an eccentrically placed nucleus, basophilic cytoplasm, and an unusually large amount of rough endoplasmic reticulum.

plasma cholesterol *(in medical biochemistry)* the concentration of cholesterol in blood plasma. In human blood, cholesterol occurs as a component of all plasma lipoproteins, but especially **very-low-density lipoprotein**, **low-density lipoprotein**, and **high-density lipoprotein**. A correlation exists between the level of plasma cholesterol and the occurrence of **atheroma** and heart attacks; this concept is associated with the role of low-density lipoprotein, which has the highest concentration of cholesterol and is thought to be the lipoprotein that distributes cholesterol to the tissues. However, the ratio of high-density lipoprotein cholesterol to low-density lipoprotein cholesterol must be taken into account, as high-density lipoprotein is thought to have a protective function in cycling cholesterol from peripheral tissues back to the liver. The circulating level of cholesterol may be altered by disturbances in carbohydrate and endocrine metabolism (e.g. diabetes or thyroid hormone imbalance), diet, and drugs. It is thought that the level of circulating total cholesterol should desirably be maintained below about 5 mmol L^{-1}.

plasma clearance *see* **clearance** (def. 2).

plasmacyte *an alternative name for* **plasma cell**.

plasmacytoma a tumour of plasma cells; most such tumours secrete myeloma proteins belonging to the same category as monoclonal antibodies.

plasma kallikrein *see* **kallikrein**.

plasmalemma *an alternative term for* **cell membrane**.

plasmalogen any glycerophospholipid in which the glycerol moiety bears an *O*-(1-alkenyl) group at position 1. The term embraces **plasmenic acid**.

plasmalogen synthase EC 2.3.1.25; an enzyme that catalyses the formation of plasmenylcholine from acyl-CoA and 1-*O*-alk-1-enyl-*sn*-glycero-3-phosphocholine with release of CoA.

plasma membrane *an alternative term for* **cell membrane**.

plasmanic acid a derivative of *sn*-glycerol 3-phosphate in which the glycerol moiety is etherified with an alkyl (or alkenyl other than 1-alkenyl) group at position 1 and esterified with an acyl group at position 2; i.e. any 2-acyl-1-*O*-R-*sn*-glycerol 3-phosphate where R = alkyl or *n*-alkenyl when $n > 1$. *Compare* **plasmenic acid**.

plasmanyl *the trivial name for* any phosphoric acyl group de-

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rived from a **plasmanic acid**. The term is useful for naming phosphoric diesters of plasmanic acid, e.g. plasmanylethanolamine, 2-acyl-1-*O*-alkyl-*sn*-glycerol 3-phosphoethanolamine. *Compare* **plasmenyl**.

plasmapheresis *or* **plasmaphoresis** *or* **plasmapharesis** *or* **plasmaphaeresis** a technique for decreasing the protein content of blood plasma circulating in the body by withdrawing blood, separating the cells by centrifugation, and then returning them to the circulation as a suspension in a suitable protein-free medium.

plasma protein **1** any of the numerous proteins present in or derived from blood plasma. **2** such proteins collectively. In mammalian plasma the concentration of plasma protein is 60–80 g L^{-1}; of this, ≈60% is serum albumin, ≈18% is immunoglobulin G, ≈9% is β_1-lipoprotein, and ≈4% is fibrinogen.

plasma thromboplastin antecedent *an alternative name for* factor XI; *see* **blood coagulation**.

plasmenic acid a derivative of *sn*-glycerol 3-phosphate in which the glycerol moiety is etherified with a 1-alkenyl group at position 1 and esterified with an acyl group at position 2; i.e. any 2-acyl-1-*O*-(1-alkenyl)-*sn*-glycerol 3-phosphate. *Compare* **plasmanic acid**, **plasmalogen**. [Contraction of plasmalogenic acid.]

plasmenyl *or (formerly)* **phosphatidal** *the trivial name for* any phosphoric acyl group derived from a **plasmenic acid**. The term is useful for naming phosphoric diesters of plasmenic acid, e.g. plasmenylethanolamine, 2-acyl-1-*O*-(1-alkenyl)-*sn*-glycerol 3-phosphoethanolamine. *Compare* **plasmanyl**.

plasmid strictly any extrachromosomal genetic element; however, mitochondrial and chloroplast DNA, yeast killer, and other cases are commonly excluded, hence the term plasmid generally refers to an extrachromosomal covalently continuous double-stranded DNA molecule that occurs in bacteria and (rarely) other microorganisms. Natural plasmids vary from ≈5 kb to over 90 kb in size. They are classified in a number of different ways: the **copy number** (between 1 and 50) describes the ratio of plasmid/chromosome molecules; the **host range** describes the variety of species that can act as host (*see also* **incompatibility**). Plasmids capable of transfer are said to be conjugal; wide host-range, conjugal plasmids are described as promiscuous. Plasmid genes include drug resistance (**resistance plasmids**), genes for catabolic enzymes (catabolic plasmids), genes for antibiotic synthesis, and genes for toxin production. Plasmids are popular choices for **cloning vectors**.

plasmid chimera a hybrid DNA molecule that has been constructed *in vitro* by joining fragments of separate plasmids and that forms a new, biologically functional replicon when inserted into a cell.

plasmid curing the elimination of a plasmid from a cell culture by treatment with **Acridine Orange** at a concentration insufficient to inhibit chromosome replication but sufficient to inhibit plasmid replication.

plasmid engineering genetic engineering when a plasmid is used as a cloning vector.

plasmid incompatibility *see* **incompatibility**.

plasmid segregation *see* **segregation** (def. 3).

plasmid transconjugant *see* **transconjugant**.

plasmid vector *see* **cloning vector**.

plasmin *or* **fibrinolysin** *or* **fibrinase** EC 3.4.21.7; a serine proteinase that converts the insoluble fibrin of a blood clot into soluble products. It is formed from **plasminogen** by proteolysis, which results in a two-chain protein linked by a single disulfide bond; the heavier A chain is derived from the N-terminal part of plasminogen and the lighter B chain contains the enzymically active site. It exhibits preferential cleavage at Lys-|-Xaa > Arg-|-Xaa bonds, with a higher selectivity than trypsin. *See also* **blood coagulation**.

plasminogen *or* **profibrinolysin** a ≈90 kDa, single-polypeptide glycoprotein found in blood plasma. It is the inactive precursor of **plasmin**, into which it may be converted by hydrolysis of one peptide bond (Arg^{560}-|-Val^{561}) brought about, e.g., by the action of **plasminogen activator** or **streptokinase**. Example from *Mus musculus* (precursor): database code PLMN_MOUSE, 812 amino acids (90.35 kDa). 3-D structure for plasminogen Kringle 4 chain a: database code NRL_1PMKA, 78 amino acids (8.90 kDa); chain b: database code NRL_1PMKB, 78 amino acids (8.90 kDa). *See also* **blood coagulation**.

plasminogen activator any serine proteinase that converts **plasminogen** into plasmin. Numerous variants occur in different tissues; they may be classified immunologically into **urokinase-type** and **tissue-type** plasminogen activators (*abbr.*: UPA and TPA respectively). Example 1, urokinase-type (EC 3.4.21.73); this catalyses specific cleavage of the Arg^{560}-|-Val^{561} bond in plasminogen to form plasmin. It is found in urine, and is used clinically for therapy of thrombotic disorders. Example from human: database code UROK_HUMAN, 431 amino acids (48.47 kDa). Example 2, tissue-type (EC 3.4.21.68); this catalyses specific cleavage of the Arg^{560}-|-Val^{561} bond in plasminogen to form plasmin. Cleavage after Arg^{310} by plasmin or trypsin results in a two-chain form of the molecule; the two halves are held together by one or more disulfide bonds. TPA is active in tissue remodelling and destruction, and particularly also in fibrinolysis, and in cell migration. Example from human: database code UROT_HUMAN, 562 amino acids (62.85 kDa). Example 3, found in certain pathogens, is the activator EC 3.4.21.–, *also known as* coagulase/fibrinolysin precursor; it is a homopentamer occurring in the outer membrane. Example from *Yersinia pestis*, the plague bacterium, in which it is involved in transmission by the insect vector (flea): database code COLY_YERPE, 312 amino acids (34.57 kDa). *See also* **urokinase**.

plasmo+ *or (before a vowel)* **plasm+** *comb. form* denoting of, pertaining to, related to, or derived from plasma.

plasmocyte *an alternative name for* **plasma cell**.

plasmodesma (*pl.* **plasmodesmata** *or* **plasmodesmas**) a fine cytoplasmic channel, found in all higher plants, that connects the cytoplasm of one cell to that of an adjacent cell. It is a roughly cylindrical, membrane-lined channel of diameter 20–40 nm, through the centre of which runs a narrower cylindrical **desmotubule**; the latter appears to be continuous with elements of the endoplasmic reticulum membrane of each of the connected cells. The function of plasmodesmata appears to be similar to that of **gap junctions** between animal cells. They permit passage of molecules of M_r less than about 800.

plasmodium (*pl.* **plasmodia**) **1** any member of the protozoan genus *Plasmodium*. Certain species parasitize humans causing malaria, while others parasitize other mammals. Their life cycle is complex, requiring, at different stages, an insect host and a mammalian host. **2** the motile multinucleate mass of protoplasm formed by the true **slime moulds** (Myxomycetes).

plasmolysis temporary shrinkage of the protoplasm of a plant or bacterial cell away from the cell wall, caused by the withdrawal of water from the cell. —**plasmolyse** *vb.*

plasmon the sum total of the extrachromosomal hereditary determinants in a cell.

plasmoptysis the localized extrusion of cytoplasm through the cell wall of a bacterium.

plasmosome *an alternative name for* **nucleolus**.

+plast *comb. form* denoting an organized subcellular particle from a living organism.

plastein a gel that may be formed on treating a partial hydrolysate of a protein with an endopeptidase. It was once thought to be a demonstration of the synthetic capability of proteinases.

plastic **1** any of a large and diverse group of polymeric materials, either synthetic or semisynthetic, that may be obtained following moulding, extrusion, etc. at a stage in their manufacture when soft or liquid. **2** made of or containing plastic; of the nature of plastic. **3** (of a material) capable of being formed or moulded. **4** *(in biology)* of or pertaining to an ability to adapt to the environment; able to change, develop, or grow. —**plasticity** *n.*

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+plastic *see* **+plasia**.

plasticizer *or* **plasticiser** any substance added to another to render the latter less brittle and/or more mouldable and flexible.

plastid any member of a family of organelles found in the cytoplasm of eukaryotic plants, all of which contain DNA, are bounded by a double membrane, and develop from a common type, the **proplastid**. Plastids also contain pigments and/or storage materials. They include **aleuroplasts**, **amyloplasts**, **chloroplasts**, **chromoplasts**, **elaioplasts**, and etioplasts.

plastidome the total complement of **plastids** of a cell.

plastocyanin a soluble protein of eukaryotic plants that contains one atom of copper per molecule and is blue in its oxidized form. It occurs in the chloroplast at a molar concentration equal to that of P700, where it functions as a one-electron carrier (E'_o = +0.43 V) between the cytochrome b_6–f and P700 of photosystem I. It is loosely bound to the inner thylakoid membrane surface. Example from pea: database code PLAS_PEA, 168 amino acids (17.14 kDa).

plastogene any of the hereditary determinants of plastids.

plastoglobuli droplets, 50–220 nm in diameter and without a bounding membrane, that occur close to thylakoid membranes in chloroplasts. Rich in lipids, particularly **plastoquinone**, they are particularly numerous when thylakoids are disrupting, and appear to be liberated therefrom.

plastome *or* **plastom** the total complement of the **plastogenes** of a cell.

plastoquinol *abbr.*: PQH_2; any hydroquinone derived from the corresponding plastoquinone by a two-electron reduction.

plastoquinone *abbr.*: PQ; any 2,3-dimethyl-5-multiprenylbenzoquinone; plastoquinones occur mainly in plants; the number of intact prenyl units in the side chain (commonly nine in the plastoquinone of higher plants) may be designated by a suffixed numeral, e.g. plastoquinone-9 (*abbr.*: PQ-9). The plastoquinone–plastoquinol redox system ($E'_o \approx +0.1$ V) functions in the electron-transport system, transferring electrons from photosystem II to the cytochrome b_6–f complex.

plate **1** *(in biology)* a Petri dish or other shallow vessel containing so-called solid or semisolid culture medium; a culture grown on this. **2** *(in chemistry)* any one of the horizontal perforated plates that comprise the fractionating component of a **plate column** for fractional distillation, or the theoretical equivalent of such a plate. *See also* **theoretical plate**. **3** *(in biology) or* **plate out** to inoculate a **plate** (def. 1) with microbial or other cells, or with material (suspected of) containing such cells. **4** to coat (a metal or other substrate) with a thin layer of (other) metal.

plateau (*pl.* **plateaux** *or* **plateaus**) **1** a part of a graph in which the value of the ordinate shows little or no change with increasing value of the abscissa. **2** a period of (relative) stability in the course of a progression. **3** to reach or pass through a plateau.

plate column *see* **plate** (def. 2).

plate height *see* **height equivalent to a theoretical plate**.

platelet *or* **thrombocyte** the smallest of the blood cells. It is an anucleate biconvex disk, 2–3 μm in diameter, formed by division of the cytoplasm of a megakaryocyte and having an exterior coat rich in glycoprotein, a normal cell membrane, and a well-developed system of microtubules some of which are arranged as an equatorial ring. The main functions of platelets are in hemostasis, by (1) adhering to damaged blood vessels and aggregating to form a plug; (2) releasing various vasoconstrictive agonists, e.g. **epinephrine**, **serotonin**, and **thromboxane A_2**; (3) activating or binding certain coagulation factors; and (4) releasing factor XIII, **platelet-derived growth factor**, and **platelet factor IV**; blood clotting then occurs around the aggregated platelets. *See* **blood coagulation**.

platelet-activating factor *abbr.*: PAF *or* PAF-acether; 1-*O*-alkyl-2-acetyl-*sn*-glycerol 3-phosphocholine, where 'alkyl' may be hexadecyl or octadecyl; a potent general inflammatory mediator, active at concentrations in the range 10^{-12} to 10^{-9} M. It is released from a variety of cells in response to a number of stimuli, e.g. by IgE-mediated release from basophils and by the interaction of tissue-bound IgG, complement, and neutrophils. It is so named because of its high activity in causing aggregation of platelets; other effects of PAF include activation of polymorphonuclear leukocytes, monocytes, and macrophages, mediation of increased vascular permeation, hypotension, decreased cardiac output, and stimulation of uterine contraction. It is synthesized in the cell in either of two ways: (1) from 1-*O*-alkyl-*sn*-glycerol-3-phosphate by addition of an acetyl group and release of phosphate, forming 1-alkyl-2-acetyl-*sn*-glycerol, which then reacts with CDPcholine to form PAF and CMP; or (2) by an alternative remodelling pathway, in which the 2-fatty acyl group is removed from a phosphatidylcholine by phospholipase A_2 and replaced with acetyl. A number of analogues act as PAF agonists, e.g. the stable analogues in which the 2-acetyl group is replaced by an ethyl, methyl, or benzyl ether group; replacement of the choline moiety by (*N*-methylpyrrolidino)-ethanolamine greatly increases its effect. PAF antagonists include gossypol, hexanolamino-PAF, *bis*(methylthio)gliotoxin, and 2,5-*bis*(3,4,5-trimethoxyphenyl)-1,3-dioxolane.

platelet basic protein precursor *abbr.*: PBP; the precursor of several peptides generated by alternative processing. Example from human: database code PF4L_HUMAN, 128 amino acids (13.88 kDa); this contains a signal (residues 1–34), platelet basic protein (35–128), **LA-PF4** (44–128), **β-thromboglobulin** (48–128), and **NAP-2** (59–128).

platelet-derived endothelial cell growth factor *abbr.*: PD-ECGF; a **cytokine** produced by platelets, fibroblasts, and smooth muscle cells. It is a monomer of 471 amino acids. A related protein, **gliostatin**, which also exists as a dimer, is produced by astrocytes. Both proteins stimulate growth of endothelial cells *in vitro* and angiogenesis *in vivo*, and promote survival and differentiation of CNS neurons; they inhibit the growth of astrocytes and glial cells. These proteins may be identical with thymidine phosphorylase.

platelet-derived growth factor *abbr.*: PDGF; a **cytokine**, of ≈30 kDa, composed of two disulfide-bonded polypeptide chains denoted A and B, which are nonidentical but homologous. It is believed that human PDGF is an AB heterodimer but pig PDGF is a homodimer of B chains. PDGF is a potent mitogen for cells of mesenchymal origin (endothelial cells, epithelial cells, some fibroblasts, smooth muscle cells) and for glial cells; it has chemotactic properties. It is released by platelets on wounding and stimulates nearby cells to grow and repair the wound; it is also produced by endothelial cells, fibroblasts, monocytes, macrophages, smooth muscle cells, and neurons. PDGF-like proteins are produced by numerous human tumour cell lines and the B chain is almost identical to part of the transforming protein produced by simian sarcoma virus (*see* ***sis***). Homodimers of A and B chains (both can bind to the receptor) are implicated in transformation processes. Examples from human (precursors); A chain (two forms, derived by alternative splicing; data refer to long form): database code PDGA_HUMAN, 211 amino acids (24.01 kDa); B chain: database code PDGB_HUMAN, 241 amino acids (27.25 kDa). *See also* **platelet-derived growth factor receptor**.

platelet-derived growth factor receptor *or* **PDGF receptor** a **tyrosine kinase** dimer, of αα, ββ, or αβ subunits, belonging to the immunoglobulin superfamily. It is a transmembrane cell surface receptor; the binding of platelet-derived growth factor (PDGF) stimulates tyrosine-kinase activity, which leads to phosphorylation of tyrosine residues in the receptor and in some cytoplasmic proteins. It belongs to a class of receptor tyrosine kinases, subclass III, that have a non-kinase insert in the cytoplasmic kinase region. Example from human (precursor); α subunit: database code PGDS_HUMAN, 1089 amino acids (122.53 kDa); β subunit: database code PGDR_HUMAN, 1106 amino acids (123.83 kDa).

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platelet endothelial cell adhesion molecule *see* **PECAM**.

platelet factor IV a 70-residue polypeptide secreted by platelets when they adhere at a site of injury. It is a **chemokine** that binds heparin strongly and is a powerful attractant for neutrophils and monocytes. Example from *Bos taurus*: database code PLF4_BOVIN, 88 amino acids (9.52 kDa).

plating *see* **plate** (def. 3, 4).

platysome *(sometimes)* the core particle of a **nucleosome**.

PLC *abbr. for* **1** preparative-layer chromatography. **2** phospholipase C; *see* **phospholipase**.

pleated sheet *see* **beta-pleated sheet**.

pleckstrin *other name*: platelet p47 protein; a platelet protein that is the major substrate for Ser/Thr phosphorylation by protein kinase C. Its function is not known. Example from human: database code P47_HUMAN, 350 amino acids (40.08 kDa). *See also* **pleckstrin homology domain**.

pleckstrin homology domain *abbr.*: PH domain; a domain first noted in the platelet protein **pleckstrin**, consisting of about 100 residues. Its function is unknown, but it has since been found in many (more than 60) proteins, especially those associated with intracellular signal transduction downstream of cell-surface receptors. It binds inositol-1,4,5-triphosphate. The 3-D solution structure of the domain from **dynamin** is known.

plectonemic coiling a type of coiling of a double-stranded helix in which the two strands are intertwined, i.e. they may not be separated without uncoiling.

pleiotropin *or* **pleiotrophin** *other name*: heparin-binding growth factor 8; a heparin-binding mitogenic protein with neurite extension activity for osteoblasts and brain cells. Example (precursor) from human: database code PTN_HUMAN, 168 amino acids (18.92 kDa).

pleiotropism *or* **pleiotropy** the phenomenon in which a single gene is responsible for producing multiple, distinct, apparently unrelated phenotypic effects; an instance of such a phenomenon. The meaning is sometimes extended to include multiple, distinct, unrelated actions or effects of a single polypeptide agonist. —**pleiotropic** *adj.*

pleiotypic relating to the process by which a single stimulus to a living cell elicits multiple, unrelated responses.

pleomorphism *or* **pleomorphy** the quality of occurring in, or exhibiting more than one distinct form. *Compare* **polymorphism**. —**pleomorphic** *adj.*

pleuropneumonia-like organism *abbr.*: PPLO; *an obsolete name for* **mycoplasma** or mollicute.

Plexiglas *or* **Plexiglass** *a proprietary name for* **poly(methyl methacrylate)**.

PLI *abbr. for* pulsed laser interferometry.

+ploid *adj. and n. comb. form* indicating the specific multiple of homologous sets of chromosomes in cell. —**+ploidy** *n.*

ploidy the number of homologous sets of chromosomes in a cell, or in each cell of an organism.

plot **1** a diagram showing the relationship between two or more variables. **2** to construct such a plot.

plotter an instrument for automatically making a **plot** (def. 1).

PLP *abbr. for* **1** pyridoxal phosphate. **2** proteolipid protein; *see* **myelin proteins**.

plug flow a type of flow of fluids in which there is no mixing in the direction of flow.

plumper a disposable, nonscratching plastic device for adding a small volume (5–50 μL) of a reagent to, and mixing it with, a liquid in a small container such as a spectrophotometer cuvette.

pluripoietin granulocyte colony stimulating factor (G-CSF) precursor. Pluripoietin α is a second human hemopoietic colony stimulating factor produced by the human bladder carcinoma cell line 5637. *See* **colony stimulating factor**.

pluripotent **1** (of a biomolecule) capable of being converted (biologically) into more than one active product. **2** (of a cell) capable of differentiating into more than one alternative type of mature cell.

plus and minus screening a technique for isolating genes for gene products that are present in one type of cell and absent in another. It involves comparing the results of **colony hybridization** of a cDNA clone library from the first cell type with cDNAs derived from the mRNAs of both cell types and then picking off the desired colonies from the reference plate.

plus end the end of a microtubule or actin filament at which addition of monomers occurs most readily; the 'fast-growing' end of a microtubule or actin filament. The plus end of an actin filament is also known as the **barbed end**.

plus strand **1** the parental polynucleotide strand in bacteriophages whose genomes consist of duplex RNA. It is the template used for the production of the complementary minus strand. **2** virus-specified messenger RNA, or any given strand of nucleic acid (RNA or DNA) whose base sequence is equivalent to that of virus-specified mRNA. Any strand having a base sequence complementary to virus-specified mRNA is described as a minus strand. **3** *(sometimes) an alternative term for* **coding strand** (of genomic duplex DNA). *Compare* **minus strand**.

pM *or* **pM** *symbol for* picomolar.

Pm *symbol for* promethium.

PMA *abbr. for* phorbol 12-myristate 13-acetate; *see* **phorbol ester**.

PMF *abbr. for* protonmotive force, *or sometimes (facetiously), after its discoverer,* Peter **Mitchell** force.

PMN *abbr. for* **1** pyridine mononucleotide. **2** polymorphonuclear (leukocyte).

pmol *symbol for* picomole.

PMR *or* **pmr** *abbr. for* proton magnetic resonance; *see* **nuclear magnetic resonance spectroscopy**.

PMS *abbr. for* **1** phenazine methosulfate. **2** pregnant mares' serum.

PMSF *abbr. for* phenylmethylsulfonyl fluoride.

PMSG *abbr. for* pregnant mares' serum gonadotropin.

PN-1 *see* **nexin 1.**

PNA *abbr. for* pentose nucleic acid (i.e. ribonucleic acid).

PNAD *abbr. for* protein NH_2-terminal arginine deamidase; an enzyme, discovered in the pig, that catalyses deamidation of N-terminal arginine residues in peptides.

pneumo+ *or* **pneumono+** *or (before a vowel)* **pneum+** *or* **pneumon+** *comb. form* of or pertaining to a lung or lungs; respiratory.

pneumococcus (*pl.* **pneumococci**) any strain of bacterium belonging to the species *Streptococcus pneumoniae*. —**pneumococcal** *adj.*

pneumococcus capsule swelling reaction *an alternative name for* **Quellung reaction**.

p[NH]ppA *symbol for* adenosine 5′-[β,γ-imido]triphosphate (alternative to Ado*PP*[NH]*P*).

PNK *abbr. for* polynucleotide kinase.

PNMT *abbr. for* phenylethanolamine *N*-methyltransferase.

PNP *abbr. for* **1** *para*-nitrophenol. **2** purine-nucleoside phosphorylase.

Po *symbol for* polonium.

pocket *(in molecular biology)* a cavity or hollow in a three-dimensional structure, e.g. a substrate pocket of an enzyme.

podocalyxin a sialated glycoprotein of the kidney glomerulus. It is the major sialoprotein of the podocyte foot process glycocalyx. It is prominently expressed on renal glomerular epithelial cells and found in patients with glomerulonephritis.

podophyllotoxin a **lignan** found in the May apple, or American mandrake (*Podophyllum peltatum*). It is known in folk medicine as a cathartic and poison, and is useful in topical treatment of warts, including venereal warts; it may have antiviral action. In mammalian cells it inhibits assembly of tubulin into microtubules, and also nucleoside transport. It is used in the synthesis of **Etoposide** and **Teniposide**.

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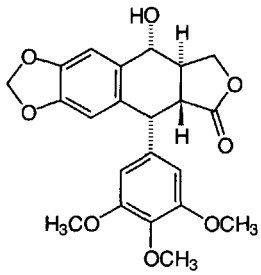

podophyllotoxin

+poiesis *noun comb. form* indicating an act or process of making (something specified), e.g. erythropoiesis, hemopoiesis. —**+poietic** *adj.*

poikilo+ *comb. form* indicating various, variable.

poikilocyte an erythrocyte that is distorted in shape and usually larger than normal, found in the blood of persons with pernicious anemia and some other anemias.

poikilosmotic describing an organism whose internal osmotic pressure varies with that of its environment. *Compare* **homoiosmotic**.

poikilothermic *or* **poikilothermal** describing an organism whose body temperature varies with that of the environment. *Compare* **homoiothermic**. —**poikilotherm** *n.*

point **1** *(in mathematics)* **a** any dimensionless geometric element whose position in space is defined by its coordinates. **b** a location or position, especially on a diagram, graph, etc. **2** a decimal point. **3** a **point of inflection**.

point group **1** a notation used in describing the geometrical arrangement of the symmetry of globular oligomeric proteins. Such molecules may belong to any of the three point groups having **cyclic symmetry**, **dihedral symmetry**, or **cubic symmetry**. **2** *(in crystallography)* a group of symmetry operations that leave unmoved at least one point within the object to which they apply. It can describe single molecules or actual crystals.

point ligand any of two or more individual atoms or groups linked covalently to a specified carbon atom in an organic compound. Point ligands may be identical or nonidentical, but they may not occupy the same position in space.

point mutation any **mutation** (def. 1) involving a single base change. *See also* **transition**, **transversion**.

point of inflection any point on a graph where the direction of curvature changes.

poise *symbol*: P; the cgs unit of dynamic viscosity; it has the dimensions of $g\ s^{-1}\ cm^{-1}$; $1\ P = 0.1\ N\ s\ m^{-2}$. [After Jean-Louis Marie Poiseuille (1799–1869), French physician and physicist.]

Poiseuille's equation an equation describing the behaviour of a liquid flowing under pressure through a capillary tube of length l and radius r. The volume flowing per second, dV/dt, is given by:

$$dV/dt = \pi Pr^4/8\eta l,$$

where η is the viscosity of the liquid and P is the pressure difference of the liquid along the tube over a distance l. [After Jean-Louis Marie Poiseuille (*see* **poise**).]

poison **1** *(in toxicology)* any substance that, in relatively small amounts, can impair the functioning of, or cause structural damage to a cell or organism. **2** *(in chemistry)* any substance that, at relatively low concentrations, inhibits a chemical reaction or inactivates a catalyst. **3** to add or administer poison to (a cell, organism, catalyst, etc.).

pokeweed mitogen *abbr.*: PWM; a plant lectin (phytoagglutinin) extractable from the roots of pokeweed, *Phytolacca americana*, a North American plant. It is one of the lectins most commonly used in immunology and cell biology. It has an affinity for *N*-acetyl-β-D-glucosamine oligomers and agglutinates leukocytes and erythrocytes (of all ABO blood groups). It also has mitogenic properties, which appear to reside in five (or more) separable components; one of these activates both T and B lymphocytes, and the others are specific for T lymphocytes.

***poky* mutant** a mutant strain of *Neurospora* with a lower rate of growth than that of wild-type strains, due to absence or deficiency of certain components of the respiratory chain. The *poky* gene appears to occur in mitochondrial DNA and is transmitted to sexually derived progeny only when the female parent exhibits the poky phenotype.

pol **1** a retroviral gene that encodes a polyprotein containing **retropepsin**, **reverse transcriptase**, and ribonuclease H (*see* **ribonuclease**). **2** as ***polA***, *polB*, *polC*, genes that encode DNA polymerases I to III.

Pol the gene product of ***polA***.

polA the structural gene in *Escherichia coli* for DNA polymerase I (Pol or Pol I; *see* **DNA polymerase**), which serves *in vivo* as a repair polymerase and as an exonuclease in the generation of **Okazaki fragments**. The enzyme belongs to family A of DNA polymerases and has three characteristic domains: 5′-exonuclease (amino acids 1–323), 3′-exonuclease (amino acids 324–517), and polymerase (amino acids 521–928). Klenow polymerase (amino acids 324–928) contains the latter two domains. *See* **Klenow enzyme**.

polar **1** pertaining to, or possessing, a **pole** or poles. **2** *(in chemistry)* (of a group or a molecular entity) having an uneven distribution of electrons and hence a permanent dipole moment. *See also* **polarity**.

polar body *(in biology)* either of the two small cells that form as a result of the division of a primary oocyte during its development to a mature ovum. One is formed in the first division of meiosis and the other in the second division of meiosis. At each division, the cytoplasm divides unequally, the polar body being of much smaller size than the developing oocyte. At the second division in which a polar body is formed, the polar body and the developing oocyte each contains a haploid set of chromosomes. The polar bodies eventually degenerate.

polar bond **1** a covalent bond in which the electron pair(s) of the bond are held with greater force by one of the two bonded atoms leading to the existence of a permanent dipole moment in the group or molecular entity in question. **2** an ionizable bond between two oppositely charged ions of a salt.

polar coordinate *(in mathematics)* either of two numbers that locate a point in a plane, one being the distance along a line to the point from the origin and the other being the angle this line makes with a fixed line passing through the origin.

polar group *see* **polar** (def. 2).

polarimeter **1** an instrument for measuring the degree of polarization of light. **2** an instrument for measuring the rotation of the plane of vibration of linearly polarized light as a result of passing through a given length of optically active material. —**polarimetric** *adj.*; **polarimetry** *n.*

polarity **1** the state, or condition, of having **poles**. **2** having a differential distribution of a property or properties along an axis; *see* **polar**. **3** having opposing physical properties at different points, e.g. north and south magnetic poles, positive and negative electric charges, hydrophobic and hydrophilic regions. **4** the state of being electrically either positive or negative. **5** (of a solvent) **ionizing power**. **6** (of an organism) the tendency to develop differentially along an axis; e.g. plants exhibit polarity in developing roots downwards and stems upwards.

polarity gradient *(in genetics)* the quantitative effect of a **polar mutation** in one gene on the expression of later genes in the operon.

polarity mutant a mutant gene formed by a **polar mutation**.

polarizability *or* **polarisability** the quality of being able to be polarized.

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polarization *or* **polarisation** 1 inducing polarity. 2 the quality of being or becoming polarized.

polarization microscope *or* **polarisation microscope** *an alternative name for* **polarizing microscope**.

polarize *or* **polarise** 1 to acquire or cause to acquire **polarity**. 2 to cause the polarization of light or other electromagnetic radiation; *see* **polarized light**. 3 to cause the electrical resistance of an electric cell to increase through the accumulation of electrolysis products at an electrode.

polarized light *or* **polarised light** light (or other electromagnetic radiation) in which the angular orientations of the electric vectors of its transverse vibrations are nonrandom. In **linearly** (or **plane-**) **polarized light** the electric vectors all lie in a given plane containing the light beam; to an observer looking along the light beam the vectors appear as a straight line through the axis of propagation. In **circularly polarized light** the angular orientations of the electric vectors are such that a given point on the vectors generates a (left-handed or right-handed) helix whose axis is the direction of the beam; to an observer looking along the light beam this point appears to describe the circumference of a circle, the light being defined as right or left circularly polarized depending on whether the point appears to the observer looking towards the source to be rotating clockwise or anticlockwise, respectively. Circularly polarized light may be considered to consist of two superimposed linearly polarized waves of equal amplitude but differing in phase by an odd number of quarter-wavelengths and having their electric vectors mutually at right angles; conversely, if right and left circularly polarized waves of equal amplitude are superimposed the resultant is a linearly polarized wave. In **elliptically polarized light** the angular orientations of the electric vectors are such that a given point on the vectors generates a (left-handed or right-handed) flattened helix whose axis is the direction of the beam; to an observer looking along the light beam this point appears to describe the perimeter of an ellipse, the degree of such polarization being characterized by the **ellipticity** and by the angular orientation of the major axis of the ellipse. Elliptically polarized light may be considered to result from the superimposition of two linearly polarized waves of equal amplitude and having their electric vectors mutually at right angles but where the phase difference is neither zero nor exactly an even or odd number of quarter-wavelengths; alternatively, it may be considered to result from the superimposition of right and left circularly polarized waves of differing amplitude.

polarizer *or* **polariser** an optical device for producing linearly polarized light, e.g. a **Nicol prism** or a sheet of **Polaroid** (def. 1).

polarizing microscope *or* **polarization microscope** a microscope that is useful for examining the birefringence properties of small objects, or for visualizing objects by virtue of their birefringence properties. *Also*: polarising microscope, polarisation microscope.

polar microtubule *see* **mitotic spindle, prometaphase**.

polar molecule a molecule in which there is a polarized distribution of positive and negative charges due to an uneven distribution of electrons. Polar molecules are likely to be soluble in water.

polar mutation a mutation in one gene that reduces the expression of genes further from the promoter in the same operon.

polarogram the current–voltage diagram obtained by **polarography**.

polarograph 1 an instrument used for **polarography**. 2 to subject (a sample) to analysis by polarography.

polarography a method for quantitative or qualitative determination of small concentrations of reducible or oxidizable substances based on the nature of the current–voltage curve obtained when a test solution is subjected to electrolysis with a steadily increasing voltage between, e.g., a dropping mercury cathode and a pool of mercury serving as anode. The current–voltage curve obtained (called a **polarographic wave**) is sigmoidal; the potential at the midpoint (called the **half-wave potential**) is characteristic of the substance being oxidized or reduced and the limiting current is related to its concentration. —**polarographic** *adj.*

Polaroid *a proprietary name for* 1 a thin, transparent material that linearly polarizes light transmitted by it (*see* **polarized light**). It consists of oriented, doubly refracting microcrystals of herapathite (quinine iodosulfate) in a matrix of cellulose acetate. 2 a photographic process or camera producing a nearly instantaneous, permanent photograph.

polar solvent any solvent of relatively high **ionizing power**.

polar zipper a motif in proteins that is considered to promote binding between protein subunits or between proteins as a result of interactions between polar residues, which are aligned in the form of a 'zip fastener'. The polar groups may consist of repeats of glutamines, Asp–Arg or Glu–Arg repeats, or repeats of glutamates and either lysines or histidines. The concept derives from the previously coined term **leucine zipper**.

pole 1 either end of an axis of rotation of a sphere or spheroid body, especially of the Earth. 2 *(in biology)* **a** either of the differentiated zones at opposite ends of an axis in a cell, organ, or organism. **b** *(in mitosis or meiosis)* either of the opposite ends of the **spindle**. 3 *(in physics)* **a** any of the zones in a magnetized body, commonly two in number and near its extremities, where the lines of magnetic flux appear to originate (**north pole**) or end (**south pole**). **b** either of the (positively or negatively charged) terminals of an electric battery, or of the corresponding terminals of a d.c. electric generator; either of two points, positions, or regions carrying opposite electric charges in a piece of material, system, or (polar or polarized) molecular entity. *Compare* **dipole**. *See also* **polar**.

policeman a device used for detaching adherent particles of precipitate, cells, etc. from the wall of a vessel and consisting commonly of a glass stirring-rod with a short piece of rubber tubing fitting tightly over one end, but sometimes of a small snipe feather cemented into the end of a capillary tube.

poly+ *comb. form* 1 denoting more than one; many or much; more than the usual number or amount; often used interchangeably with **multi+**. 2 indicating heterogeneity of a physical attribute e.g. polychromatic, polydisperse. *Compare* **mono+** (def. 2). 3 *(in chemistry and biochemistry)* **a** denoting more than one of a specified component or substituent, e.g. polyamine, polyene, polyester; in names of large molecules, usually denoting more than 10–20 of the component specified, especially in contrast to **oligo+** (def. 2), e.g. polynucleotide, polypeptide, polysaccharide. *Compare* **mono+** (def. 3). **b** denoting polymer of a specified substance, e.g. polyglycine, polystyrene. **c** indicating more than one function of the kind specified, e.g. polyacidic, polybasic, polydentate, polyhydric. *Compare* **mono+** (def. 5).

poly(A) *abbr. for* polyadenylate.

polyacidic (of a **base** (def. 1)) able to accept more than one proton per molecule in solution.

polyacrylamide (gel) *a common name for* any hydrogel containing a three-dimensional matrix of randomly cross-linked polymers of acrylamide (2-propenamide; CH_2=CH–CO–NH_2). The cross-linking agent commonly used is *N,N′*-methylene bisacrylamide, (CH_2=CH–CO–NH)$_2CH_2$, polymerization being initiated by various alternative methods for generating free radicals. The pore size and rigidity of the gel depend on the concentration of acrylamide and the proportion of cross-linking agent used.

polyacrylamide gel electrophoresis *abbr.*: PAGE; a technique of **zone electrophoresis** that uses polyacrylamide gel as supporting medium. It is especially useful for the separation of biopolymers and fragments thereof. A two-dimensional electrophoresis has been used to resolve as many as 1000 proteins: in the first step the polypeptides are separated by **isoelectric focusing electrophoresis** and in the second step by **SDS (polyacrylamide) gel electrophoresis**. The 2-D process was devised by P. H. O'Farrell, after whom it is often named.

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polyacrylamide gradient gel electrophoresis *an alternative name for* **gradient gel electrophoresis**.

polyadenylate **1** *abbr.*: poly(A); any homopolymer of adenylate (i.e. adenosine 5′-monophosphate). Most eukaryotic mRNAs are terminated at the 3′ end by a tract of poly(A) 40–200 residues long (*see* **poly(A) tail**). **2** to add a stretch of polyadenylate to a molecule. —**polyadenylation** *n.*

poly(ADP-ribosyl) a structure found attached to histones H1 and H2B, to other eukaryotic chromosomal proteins, and to some mitochondrial proteins. It consists of a polymer of 20–50 ADP-D-ribosyl units linked by glycosidic bonds; linkage is formed by transfer of the ADP-ribosyl unit of NAD^+, linking its ribosyl C-1 position to the C-2′ position of the ribosyl of the terminal ADP-ribose of the growing chain. The attachment to protein appears, at least in some instances, to be through an ester linkage between the terminal ribose group and certain free carboxyl groups in the protein. *See also* **ADP-ribosylation**; **NAD(P)$^+$–arginine ADP-ribosyltransferase**.

poly(ADP)-ribosyl transferase EC 2.4.2.30; *recommended name*: NAD^+ ADP-ribosyltransferase; *systematic name*: NAD^+:poly(adenine-diphosphate-D-ribosyl)-acceptor ADP-D-ribosyl-transferase; *other names*: poly(ADP) polymerase; poly(adenosine diphosphate ribose) polymerase; ADP-ribosyltransferase (polymerizing); poly(ADP-ribose) synthetase. An enzyme responsible for ADP-ribosylation of acceptors; it catalyses a reaction between NAD^+ and $(ADP\text{-D-ribosyl})_n$-acceptor to form nicotinamide and $(ADP\text{-D-ribosyl})_{n+1}$-acceptor. It often has zinc as cofactor (as in example); the acceptor is a histone or the enzyme itself. The modification is dependent on DNA and is involved in the regulation of cellular processes such as differentiation, proliferation, and tumour transformation and also in the regulation of the molecular events involved in the recovery of a cell from DNA damage. Example from human: database code PPOL_HUMAN, 1013 amino acids (112.82 kDa). *See also* **NAD(P)$^+$–arginine ADP-ribosyltransferase**. *Compare* **ADP-ribosylation**.

polyamide any polymer in which the constitutional units are joined by amide or thioamide links. *Compare* **nylon**, **polypeptide**.

polyamine any organic compound containing two or more amino groups. **Putrescine**, **spermine**, and **spermidine** are important animal polyamines. Polyamines are synthesized by various routes. In animals, **putrescine** is the decarboxylation product of **ornithine**. Decarboxylated *S*-adenosylmethionine (*see* **S-adenosylmethionine decarboxylase**) is a substrate in a reaction in which propylamine is transferred to putrescine to form spermidine, and again to spermidine to form spermine. *See also* **ornithine decarboxylase**.

poly(amino acid) any homopolymer, or mixture of homopolymers, of a particular (specified) amino acid.

polyampholyte any amphoteric **polyelectrolyte**.

polyanion any macromolecular ion that carries multiple negative charges.

poly(A) polymerase *abbr.*: PAP; *the recommended name for* **polynucleotide adenylyltransferase**.

poly(A) tail a sequence of adenylyl residues at the 3′ end of eukaryotic mRNA. Almost all mature eukaryotic mRNAs have 3′-poly(A) tails of 40–200 nucleotides, those of histones being a notable exception. The poly(A) tail is added enzymically to the primary transcript, which is first cleaved 10–30 nucleotides past a highly conserved AAUAAA sequence. The poly(A) tail is then generated from ATP through the action of **polynucleotide adenylyltransferase**. In practical terms the poly(A) tail on mRNA has facilitated its ready isolation from total cellular RNA by affinity chromatography on oligo(dT)-cellulose.

polyatomic (of a molecular entity) composed of two or more atoms.

polybasic (of an **acid** (def. 1)) able to give up more than one proton per molecule in solution.

poly(C) *abbr. for* polycytidylate.

polycarbonate any polymer in which the structural units are linked by carbonate ester groups, usually formed by the polymerization of diphenylols with phosgene (i.e. carbonyl chloride). Such polymers are tough thermoplastic resins.

polycation any macromolecular ion that carries multiple positive charges.

polychromatic **1** relating to, or possessing, various or varying colours; consisting of, relating to, or emitting light (or other electromagnetic radiation) of two or more frequencies or wavelengths. **2** of, relating to, or showing **polychromatophilia**.

polychromatophilia the quality of being stainable by more than one type of dye, especially by both acid and basic dyes.

polycistronic messenger RNA *or* **multicistronic messenger RNA** *or* **polygenic messenger RNA** any messenger RNA molecule that carries more than one initiation site and encodes the synthesis of two or more (usually related) gene products. It is formed by transcription of a single operon and is characteristic of prokaryotes.

polyclonal of, pertaining to, being formed by, or derived from two or more **clones** (def. 1).

polyclonal antibody an antibody that arises from the immune response to an immunogen. Each **epitope** on the immunogen has the potential for causing the formation of a clone of **B lymphocytes** each capable of synthesizing an antibody specific to the particular epitope.

polycyclic having more than one ring of atoms in the molecule; used especially of molecules with condensed ring systems.

polydentate *an alternative term for* **multidentate**.

polydeoxynucleotide *or* **polydeoxyribonucleotide** any **polynucleotide** composed solely of **deoxynucleotide** residues.

polydisperse describing a colloidal system whose disperse phase consists of particles of many different sizes. —**polydispersity** *n.*

polyelectrolyte any macromolecular substance that, on dissolution in water or another ionizing solvent, dissociates to give polyanions or polycations together with an equivalent of oppositely charged ions, which may be simple ions or themselves polyions.

polyene any unsaturated organic compound containing two or more carbon–carbon double bonds.

polyene antibiotic any member of a group of structurally related antibiotics produced by *Streptomyces* spp. They possess a large lactone ring containing 4–7 conjugated double bonds (generally all-*trans*) and substituted by aliphatic groups, by a residue of **mycosamine** or another amino sugar, and by numerous hydroxyl groups. The polyene antibiotics include **amphotericin B** and **nystatin**; they interact with sterols in cell membranes and hence have antifungal but not antibacterial activity and tend to be toxic to mammals. *Compare* **macrolide**.

polyenoic acid any alkenyl carboxylic acid containing two or more double bonds per molecule.

polyester any synthetic polymer in which the constitutional units are joined by ester bonds; proprietary materials include Dacron and Mylar. Polyesters are extensively used in textiles, ropes, etc.

polyethylene *an alternative name (esp. US) for* **polythene**. *See also* **polyethylene glycol**.

polyethylene glycol *abbr.*: PEG; any polymer of general formula $H(OCH_2CH_2)_nOH$, where $n \geq 4$; a suffixed number may be used as a guide to the average relative molecular mass, e.g. polyethylene glycol 4000. Polyethylene glycols are clear viscous liquids or white solids, useful as embedding media for microscopy, as bases for ointments, and in radioimmunoassays.

poly(ethyleneimine) a water-soluble synthetic linear polymer of ethyleneimine (i.e. aziridine) of 30–40 kDa. It is useful for the selective precipitation of proteins and nucleic acids. It is also used as a substituent in hydroxylated chromatographic support matrices, as in PEI-cellulose, to form anion exchangers. *Proprietary name*: Polymin P.

polyfructosan *former term for* **fructan**.

poly(G) *abbr. for* polyguanylate.

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polygalactan *former term for* **galactan**.

polygalacturonase EC 3.2.1.15; *other name*: pectinase; an enzyme that hydrolyses 1,4-α-D-galactosiduronate linkages in pectin and other galacturonans in a random fashion. It participates in cell-wall degradation in plants. Example, polygalacturonase I precursor from *Aspergillus niger*: database code PGL1_ASPNG, 368 amino acids (38.11 kDa).

polygene any one of a group of genes, each of which individually exerts a small effect on the phenotype but that together control a quantitative character such as stature.

polygenic describing a character or trait that is controlled by polygenes. *Compare* **multigenic**.

polyglucosan *a former term for* **glucan**.

polygon any closed plane figure bounded by three or more (nonintersecting) straight lines. —**polygonal** *adj.*

polyhedron (*pl.* **polyhedrons** *or* **polyhedra**) any solid figure bounded by four or more plane faces, each of which is a polygon. —**polyhedral** *adj.*

polyhydric describing any chemical compound containing two or more hydroxyl groups per molecule; used especially of alcohols.

poly(hydroxybutyrate) a linear polymer of approximately 1500 (*R*)-3-hydroxybutyrate residues held together in ester linkage. It is found in the cells of a number of prokaryotic genera where it occurs in membrane-bound granules and acts as a storage material.

poly(I) *abbr. for* polyinosinate.

polyion any macromolecular ion that carries multiple charges.

polykaryocyte a multinucleate cell. —**polykaryotic** *adj.*

polyketide *or (sometimes)* **acetogenin** any of a diverse group of natural products synthesized via linear poly-β-ketones, which are themselves formed by repetitive head-to-tail addition of acetyl (or substituted acetyl) units indirectly derived from acetate (or a substituted acetate) by a mechanism similar to that for fatty-acid biosynthesis but without the intermediate reductive steps. In many cases, acetyl-CoA functions as the starter unit and malonyl-CoA as the extending unit. Various molecules other than acetyl-CoA may be used as starter, often with methylmalonyl-CoA as the extending unit. The poly-β-ketones so formed may undergo a variety of further types of reaction, which include alkylation, cyclization, glycosylation, oxidation, and reduction. The classes of product formed – and their corresponding starter substances – comprise *inter alia*: coniine (of hemlock) and orsellinate (of lichens) – acetyl-CoA; flavanoids and stilbenes – cinnamoyl-CoA; tetracyclines – amide of malonyl-CoA; urushiols (of poison-ivy) – palmitoleoyl-CoA; erythronolides – propionyl-CoA and methylmalonyl-CoA as extender.

polylabelling labelling where more than one atom of a molecule has been isotopically substituted.

polylinker any **linker** containing multiple restriction sites.

polymannan *a former term for* **mannan**.

polymer **1** *(in chemistry and biochemistry)* any substance that is composed of molecules containing a large number of constitutional units (or 'mers') that are in repetitive covalent linkage and that may be of one or more than one species. Polymers are generally considered to comprise at least ten mers, although sometimes the term is taken to imply simply 'more than one' mer. Hence 'polymer' may or may not embrace **oligomer**, depending on the branch of chemistry or biochemistry concerned. **2** *(in molecular biology and enzymology) (sometimes) an alternative term for* **multimer**. *See also* **heteropolymer**, **homopolymer**. —**polymeric** *adj.*; **polymerize** *or* **polymerise** *vb.*; **polymerization** *or* **polymerisation** *n.*

polymerase *a general name for* any of various enzymes (transferases) catalysing the formation of biological **polymers** (def. 1), especially of polynucleotides. *See* **DNA polymerase**, **RNA polymerase**.

polymerase accessory protein any of a group of proteins that are associated with **DNA polymerases**. Examples (1) DNA polymerase α binding factor from yeast: database code CTF4_YEAST, 926 amino acids (104.18 kDa); (2) phage T4 accessory proteins: protein 44, database code DPA4_BPT4, 319 amino acids (35.74 kDa); protein 45, database code DPA5_BPT4, 227 amino acids (24.80 kDa); protein 62, database code DPA6_BPT4, 187 amino acids (21.34 kDa).

polymerase chain reaction *abbr.*: PCR; a method whereby a specific sequence of nucleotides within a double-stranded DNA is amplified. The sequence is identified by the use of short synthetic oligonucleotides that are complementary to the two terminal regions of the DNA sequence to be amplified; these oligonucleotides are extended by the thermostable ***Taq* DNA polymerase** on the DNA template. The effect is that the new chains span the region delimited by the two chosen termini. The nascent chains are heat denatured and the process is repeated. Up to 100 000-fold **amplification** of the DNA stretch required may be obtained. The method was first described by Kary B. **Mullis** in 1984. The use of the thermostable *Taq* polymerase from a thermophilic bacterium avoids the need to add more polymerase at each cycle because the enzyme is not inactivated at the temperature of denaturation of the DNA. PCR amplification has become an indispensable tool in a great variety of applications. Clinically it may be used for the rapid diagnosis of infectious diseases and the detection of rare mutations associated with cancer. Forensically, the DNA from even a single hair or sperm can be used to identify the donor. RNA may be amplified by first converting it to cDNA through the use of reverse transcriptase.

polymetaphosphate *(sometimes) an alternative name for* **polyphosphate**.

poly(methyl methacrylate) a clear, easily worked, relatively nontoxic thermoplastic, useful as a substitute for glass and in the construction of many pieces of scientific apparatus. *Proprietary names*: Lucite, Perspex, Plexiglass, etc.

Polymin P *a proprietary name for* **poly(ethyleneimine)**.

polymorph *see* **polymorphonuclear leukocyte**.

polymorphic *or* **polymorphous** having, assuming, or passing through various different forms or styles; exhibiting or undergoing **polymorphism**.

polymorphism **1** *(in biology)* **a** the occurrence of two or more distinct kinds of individual (**morphs**) belonging to the same species within a population that is interbreeding freely. **b** **genetic polymorphism**. **2** *(in chemistry)* the existence of the same substance in two or more different crystalline forms. *See also* **enantiomorph**.

polymorphonuclear **1** describing a cell whose nucleus is multipartite or **polymorphic**. **2** a **polymorphonuclear leukocyte**.

polymorphonuclear leukocyte *or* **polymorphonuclear** *or* **polymorph** *abbr.*: PMN; any white blood cell of the myeloid series that in its mature form has a lobed and variably shaped nucleus and granular cytoplasm; included are basophil leukocyte, eosinophil leukocyte, and neutrophil leukocyte. The term is often used erroneously for neutrophil leukocyte solely.

polymorphous *a variant form of* **polymorphic**.

polymyxin any of a group of related antibiotics isolated from cultures of *Bacillus polymyxa* and active against most Gram-negative bacteria. Individual polymyxins are designated by suffixed letters, e.g. polymyxin B. All are decapeptides containing five or six residues of L-2,4-diaminobutyric acid. Their biosynthesis does not involve ribosomes (*see* **protein and peptide biosynthesis**). The sequence of seven residues at the C-terminal end is formed into a heterodetic ring through an isopeptide link to one of the diaminobutyric acid residues, while the N-terminal residue is acylated with a 6-methylheptanoyl or 6-methyloctanoyl group. Polymyxins bind to the cytoplasmic membrane of sensitive organisms, causing leakage of cytoplasmic components; however, they also attack the cell membranes of eukaryotic cells and therefore have limited clinical usefulness; they are used in antibiotic ointments. Polymyxin B inhibits protein kinase C. *See also* **colistin**.

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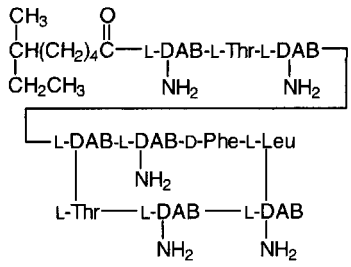

polymyxin B1
DAB = diaminobutyric acid

polynucleate *or* **polynuclear** (of a cell) containing several or many nuclei; **multinucleate**.

polynucleotidase *an alternative name for* **polynucleotide phosphatase**.

polynucleotide any one-stranded homo- or heteropolymer of at least about ten **nucleotide units** connected by phosphodiester linkages between (usually) the 3′ position on the glycose moiety of one nucleotide unit and the 5′ position on the glycose moiety of the adjacent one, or any two-stranded molecule comprised of two such one-stranded molecules held together by hydrogen bonds. Comprehends the term **nucleic acid**.

polynucleotide adenylyltransferase EC 2.7.7.19; *other names*: NTP polymerase; RNA adenylating enzyme; poly(A) polymerase; an enzyme that adds the **poly(A) tail** to mRNA. It catalyses a reaction of the type:

$$n\ \text{ATP} + (\text{nucleotide})_m = n\ \text{pyrophosphate} + (\text{nucleotide})_{m+n}.$$

PAP I and II are long forms of the enzyme that contain four functional domains: a ribonucleoprotein-type RNA-binding domain, a catalytic region, two nuclear localization signals, and a C-terminal serine/threonine-rich region. Clones of a number of truncated forms have been obtained, some of which are expressed in tissues. Examples from vaccinia virus subunits PAP1 (VP55) and PAP2 (VP39): database codes PAP1_VACCC, 479 amino acids (55.52 kDa), and PAP2_VACCC, 333 amino acids (38.87 kDa). Example from yeast: database code PAP_YEAST, 568 amino acids (64.48 kDa). The enzyme from *Escherichia coli* (also known as **plasmid copy number protein**): database code PCNB_ECOLI, 468 amino acids (53.81 kDa). *See also* **polyadenylate**.

polynucleotide kinase *abbr.*: PNK; any of a number of enzymes belonging to subclass EC.2.7 that phosphorylate the 5′ end of nucleic acids. The reaction is between ATP and the 5′-OH of RNA or DNA to form ADP and RNA or DNA-5′-phosphate. Example, phage T4 enzyme: database code KIPN_BPT4, 301 amino acids (34.58 kDa).

polynucleotide ligase *an alternative name for* DNA ligase (ATP); *see* **DNA ligase**.

polynucleotide ligase (NAD$^+$) *an alternative name for* DNA ligase (NAD$^+$); *see* **DNA ligase**.

polynucleotide phosphatase *or* **polynucleotidase** either of the enzymes polynucleotide 3′-phosphatase (EC 3.1.3.32) or polynucleotide 5′-phosphatase (EC 3.1.3.33).

polynucleotide phosphorylase *an alternative name for* polyribonucleotide nucleotidyltransferase (EC 2.7.7.8).

polyol any polyhydric alcohol.

polyol (metabolic) pathway *(sometimes)* a metabolic pathway by which nonphosphorylated sugars and sugar alcohols are interconverted.

polyomavirus any member of a genus (*Polyomavirus*) of mouse viruses of the Papovaviridae family. They are widely distributed and may be oncogenic under appropriate conditions.

polyose *an obsolete term for* any polymer consisting of an unknown or unspecified number of covalently linked monose residues.

polypeptide **1** any peptide comprising more than about 10–20 amino-acid residues connected by peptide linkages. Unlike a **protein** it usually lacks appreciable tertiary structure in solution and is not liable to irreversible denaturation. **2** *(loosely) an alternative term for* **protein**. **3** describing another entity of a polypeptide nature, e.g. polypeptide chain, polypeptide hormone.

polypeptide hormone *an alternative term for* **peptide hormone**.

polyphase *or* **polyphasic** **1** (of matter) consisting of two or more phases. **2** *or* **multiphase** (of an electrical system or device) having, generating, or using two or more alternating electric voltages of the same frequency but differing from each other in phase. **3** (of a process) consisting of or occurring in a number of separate stages.

polyphenol oxidase EC 1.10.3.1; *recommended name* catechol oxidase; any of a family of copper-containing oxidoreductases that catalyse the oxidation of mono and *o*-diphenols to *o*-diquinones. These enzymes are found in plants, localized in membranes of plastids, but their normal function is unknown. However, they are responsible for brown discoloration ('browning') in fruit and vegetables on storage, as their products give rise, probably nonenzymatically, to polyphenolic melanin-like compounds. Sequences of polyphenol oxidase genes from different plants are very similar, but when compared with related bacterial, fungal, or animal enzymes (*see* **monophenol monooxygenase**) only the putative copper-binding sites are conserved. Example from *Lycopersicon esculentum* (tomato), polyphenol oxidase B precursor: database code PPOB_LYCES, 596 amino acids (67.23 kDa).

polyphosphate *or (sometimes)* **polymetaphosphate** **1** any ionic form of polyphosphoric acid, $H_{n+2}P_nO_{3n+1}$ (where n is an unknown or unspecified integer greater than 1), or any mixture of polyphosphoric acid and its ionized forms. Polyphosphate occurs in the **volutin granules** observed in many microorganisms, where it is synthesized by the action of the enzyme **polyphosphate kinase** and is believed to serve as a phosphate store. **2** any (partial or full) salt or ester of polyphosphoric acid. *See also* **metaphosphate**.

polyphosphate kinase EC 2.7.4.1; a microbial enzyme that catalyses the synthesis of **polyphosphate** by transfer of the terminal phosphoric residue of ATP to diphosphate (i.e. pyrophosphate) or to a polyphosphate one residue smaller than the product. Example from *Klebsiella aerogenes*: database code PPK_KLEAE, 684 amino acids (80.03 kDa).

polyphosphoinositide *or* **polyphosphatidylinositide** *a former inappropriate general name for* any [mono]phosphate, bisphosphate, trisphosphate, or tetrakisphosphate of phosphatidylinositol; use not recommended.

polyploid describing a cell (or organism) that has three, four, five, or more times the haploid number of chromosomes in its nucleus. —**polyploidy** *n.*

polyprenol *a recommended term for* any **prenol** in which there are more than four isoprene residues; the isoprene units may be all-*trans* or a mixture of *cis* and *trans*. The number of such units in a particular polyprenol may be indicated by a multiplicative prefix, e.g. undecaprenol. Polyprenols and their derivatives are widely distributed in living organisms. *See also* **dolichol**.

polyprenyl the univalent alkyl group derived from a **polyprenol** by loss of its hydroxyl group. The number of isoprene residues in a particular polyprenyl derivative may be indicated by a multiplicative prefix, e.g. undecaprenyl diphosphate.

polyprotein any polypeptide that on cleavage gives rise to two or more biologically active proteins, e.g. **proopiomelanocortin**.

polyribonucleotide any polynucleotide composed solely of ribonucleotide residues.

polyribonucleotide nucleotidyltransferase EC 2.7.7.8; *other name*: polynucleotide phosphorylase. An enzyme that is

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involved in the degradation of mRNA, hydrolysing single nucleotides successively from the 3′ end of the RNA, to yield a nucleoside diphosphate and a shortened mRNA. Example from *Escherichia coli*: database code PNP_ECOLI, 711 amino acids (77.10 kDa).

polyribonucleotide synthase (ATP) *see* **RNA ligase (ATP)**.

polyribosome *an alternative name for* **polysome**.

polysaccharide *an alternative name for* **glycan**; i.e. any linear or branched polymer consisting of monosaccharide residues. Important polysaccharides include glycogen, starch, hyaluronic acid, and cellulose.

polysome *or* **ergosome** *or* **polyribosome** any structure consisting of two or more ribosomes attached to different points on the same strand of messenger RNA. Hence, a polysome is a complex involved in the cellular synthesis of the polypeptide specified in the message. Polysomes effect the synthesis of all proteins, but in the case of secretory proteins they become attached to the **rough endoplasmic reticulum**.

polysomic **1** describing a cell or organism that has one or more normal chromosomes in excess of the usual diploid or polyploid complement; being such a chromosome. **2** a polysomic organism. **—polysomy** *n.*

polystyrene phenylethene homopolymer; a clear, brittle, rigid thermoplastic with high electrical resistivity. A proportion of divinylbenzene may be added as a cross-linking agent during polymerization in order to produce polystyrene resins of various porosities for use in the preparation of polystyrene ion-exchange resins.

polysubstituted having more than one chemical substituent. **—polysubstitution** *n.*

poly(T) *abbr. for* polythymidylate.

polytene chromosome a type of chromosome in a **polyploid** cell, formed when multiple copies of homologous chromosomes are aligned side by side to give a giant chromosome in which distinct chromosome bands are readily visible.

polyteny *an alternative name for* **endomitosis**. **—polytene** *adj.*

polytetrafluoroethylene *abbr.*: PTFE; tetrafluoroethene homopolymer; a polymer consisting of chains of (≈2000) linked $-CF_2-$ units prepared by polymerization of tetrafluoroethylene, $F_2C{=}CF_2$. It is a nonflammable thermoplastic, extremely chemically resistant, of high electrical resistivity, and with an extremely low coefficient of friction. It is useful as tubing and sheeting in chemical laboratory work, as a lining to reaction vessels, as gasket material, and as packing for pumps and bearings. *Proprietary names*: Fluon, Teflon, etc.

polythene *or (esp. US)* **polyethylene** ethene homopolymer; a versatile thermoplastic polymer of ≈1.5–100 kDa, prepared by polymerization of ethylene. **High-density polyethylene**, a linear polymer, is fairly rigid and crystalline, while **low-density polyethylene**, a branched polymer, is softer and more flexible; both forms are chemically resistant and have high electrical resistivity.

polytopic describing an integral membrane protein that completely traverses the membrane two or more times.

polytrioxophosphate(v) *the recommended name for* **metaphosphate**.

poly(U) *abbr. for* polyuridylate.

polyubiquitin the form in which **ubiquitin** (def. 1) is synthesized, a precursor with a number of head-to-tail repeats.

polyunsaturated describing a substance containing more than one carbon–carbon multiple bond per molecular entity or residue; applied especially to a fatty acid containing more than one multiple bond in the hydrocarbon chain of its molecular structure, and to a fat or oil derived from one or more such fatty acids. *See also* **polyunsaturated fatty acid**. **—polyunsaturation** *n.*

polyunsaturated fatty acid *abbr.*: PUFA; any fatty acid that is **polyunsaturated**; the multiple bonds are most frequently all ethylenic and usually methylene-interrupted, the configuration of their substituents generally being *Z* (i.e. *cis*); more rarely is an acetylenic bond present. In animal metabolism polyunsaturated fatty acids belong to families denoted by the position of the double bond nearest to the methyl group and often also by the name of the fatty acid from which the remainder can be derived; hence **linoleic family**, **linolenic family**, **oleic family**, and **palmitoleic family**. In recent years, emphasis has been placed on a role of some polyunsaturated fatty acids in lowering plasma cholesterol, and potentially reducing the risk of heart disease. Foremost among these have been those of the *n*-6 family such as linoleic acid. A recommendation has been made that the diet should contain these polyunsaturated fats in a ratio of 2:1 to saturated fats. *See also* **essential fatty acid**, **fatty-acid nomenclature**, **fish oil**.

polyuria the passing of large volumes of urine.

polyuronide *an old term for* **glycuronan**.

polyvalent *or* **multivalent** **1** *(in chemistry)* **a** having a numerical valency greater than unity. **b** capable of exhibiting more than one valency value. **2** *(in immunology)* **a** (of an antibody molecule or fragment) having at least two combining sites. **b** (of an antiserum or other antibody preparation) capable of combining with two or more different antigens. **c** (of a vaccine) capable of eliciting immunity to more than one (strain of) microorganism, toxin, or other antigenic agent.

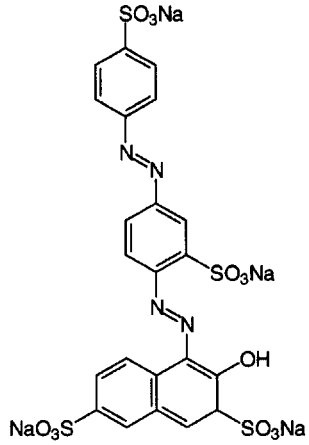
polyvinyl acetate *abbr.* PVA; ethenoic acid homopolymer; a synthetic polymer obtained from ethyne and acetic acid, used in adhesives and paints and in the manufacture of polyvinyl alcohol.

polyvinyl alcohol *abbr.*: PVA; ethenol homopolymer; a polymer prepared from polyvinyl acetates by replacement of the acetate groups by hydroxyl groups; the commercial products have differing contents of residual acetyl groups and hence differing physical characteristics. Polyvinyl alcohols are used in adhesives and can also be compounded into elastomers, which are useful in the manufacture of artificial sponges, hydrocarbon-resistant tubing, etc.

polyvinyl chloride *abbr.*: PVC; chloroethene homopolymer; a plastic solid, soluble in many organic solvents, that discolours on exposure to light or heat unless containing stabilizers. It is useful for the manufacture of rubber substitutes and electric wire coverings.

polyvinyl pyrollidone *abbr.*: PVP; 1-ethenyl-2-pyrridinone homopolymer; commercial preparations are ≈10 kDa to ≈700 kDa; it is soluble in water to give colloidal solutions. PVP is used in the preparation of enzymes from plants; it removes phenolic compounds that can destroy enzyme activity.

polyxenic *see* **synxenic**.



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pomace the pulpy residue remaining after extraction of juice from fruits such as apples, or after extraction of oil from seeds, nuts, or similar materials.

POMC *abbr. for* proopiomelanocortin.

Pompe's disease *an alternative name for* type II glycogen (storage) disease; *see* **glycogen disease**.

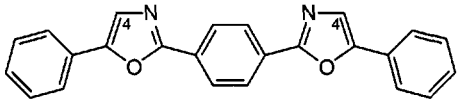
Ponceau S *or* **Fast Ponceau 2B** a dye used for staining protein, especially on cellulose acetate strips. (Illustrated on p. 523.)

pontal (of an atom or group) bridging.

ponticulin an F-actin-binding transmembrane glycoprotein of plasma membranes of the cellular slime mould *Dictyostelium discoideum*. It is a major membrane protein of this organism and a protein of the major high-affinity actin–membrane link. It is directly involved in actin polymerization. Example: database code A54793, 143 amino acids (14.75 kDa).

pool *see* **metabolic pool**.

POPOP 1,4-bis(5-phenyloxazol-2-yl)benzene; a secondary fluor used in liquid scintillation counting, originally as a wavelength shifter and more recently to decrease sensitivity to the action of quenching agents.



population **1** *(in biology)* any group of individual organisms of the same species inhabiting a given area; the number of such individual organisms. **2** *(in statistics) or* **universe** any finite or infinite collection of individuals or items from which a sample has been drawn.

population standard deviation *see* **standard deviation**.

P:O ratio *abbr. for* phosphorus:oxygen ratio.

porcine *abbr. (in compound abbrs.)* p *or (formerly)* P; of, characteristic of, or relating to a pig or pigs; resembling a pig.

pore any very small opening, e.g. in a (cell) membrane or in the integument of an organism, that allows the passage of gases and/or liquids.

porin **1** any member of a class of similar proteins of ≈15 kDa (monomer) that can be isolated from the outer membranes of certain Gram-negative bacteria. Trimers of these proteins are thought to make these membranes porous to hydrophilic substances of ≤600 Da by forming in them water-filled channels that allow transmembrane diffusion of uncharged small solutes. The proteins are usually homotrimers with several characteristic motifs; they are typically beta barrels with short α-helical domains. Examples: (1) from *Rhodobacter capsulatus*: database code NRL_2POR, 301 amino acids (31.50 kDa); 3-D structure known; (2) from *Escherichia coli* (*Neisseria* protein is similar): database code PHOE_ECOLI, 351 amino acids (38.88 kDa). **2** any of the transmembrane proteins typically of the mitochondrial outer membrane in eukaryotes that form aqueous channels through the lipid bilayer, allowing passage of small molecules. These constitute a structural family, characterized by four motifs and much β structure. Human mitochondrial membrane porin (voltage-dependent anion-selective channel protein) allows diffusion of small hydrophilic molecules; the channel adopts an open conformation at low or zero membrane potential and a closed conformation at potentials above 30–40 mV. Example: database code PORI_HUMAN, 282 amino acids (30.61 kDa).

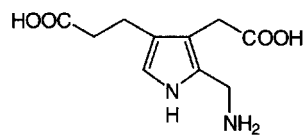
porosity **1** the state or quality of being **porous**. **2** the degree to which a material or substance is porous.

porosome nuclear pore complex.

porous having pores; allowing the passage or uptake of gases and/or liquids, especially by diffusion rather than by bulk flow.

porphin *or* **porphine** *an alternative name for* **porphyrin** (def. 1).

porphobilinogen *abbr.*: PBG; 5-(aminomethyl)-4-(carboxymethyl)-1*H*-pyrrole-3-propanoic acid; the biosynthetic precursor of all porphyrins. It is excreted in relatively large amounts in the urine in some porphyrias.



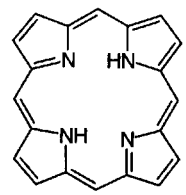
porphobilinogen deaminase *see* **hydroxymethylbilane synthase**.

porphobilinogen synthase EC 4.2.1.24; *systematic name*: 5-aminolevulinate hydro-lyase (adding 5-aminolevulinate and cyclizing); *other names*: δ-aminolevulinic acid dehydratase; aminolevulinate dehydratase. An enzyme that catalyses the conversion of two moles of 5-aminolevulinate to one mole of porphobilinogen + 2 H_2O in the pathway for the synthesis of **porphyrins**; zinc is a cofactor. Example from *Escherichia coli*: database code HEM2_ECOLI, 323 amino acids (35.45 kDa).

porphyr+ *a variant form of* **porphyro+** (before a vowel).

porphyria any of a group of metabolic disorders characterized by the excretion of abnormally large amounts of various porphyrins and/or their biosynthetic precursors. Porphyrias are currently classified as primary (if inherited) or secondary (if acquired). The primary disorders may be further classified into two broad categories: (a) the neurological/psychiatric forms and (b) the forms associated with cutaneous photosensitivity, though these two types of symptoms may in some cases overlap. The acquired disorders are much more common than the inherited conditions. There is no clear-cut association of enzyme defects with specific porphyrias. Elevated blood levels of intermediates in porphyrin biosynthesis are normally present during attacks. Elevated intermediates that are found, together with (in parentheses) associated enzymes and conditions are (1) aminolevulinic acid (or ALA) (porphobilinogen (or PBG) synthase; PBG synthase deficiency porphyria); (2) ALA and PBG (PBG deaminase; acute intermittent porphyria, variegate porphyria); (3) uroporphyrin (uroporphyrinogen decarboxylase; porphyria cutanea tarda, acute intermittent porphyria) (4) coproporphyrin (coproporphyrinogen oxidase; variegate porphyria, hereditary coproporphyria). Acquired porphyria may be due to lead exposure, some malignancies, and chronic ethanol exposure among other causes. It has been suggested that the British king, George III, suffered from a form of porphyria leading to psychiatric symptoms.

porphyrin **1** *the systematic name for* the fundamental skeleton, $C_{20}H_{14}N_4$, of the macrocyclic **tetrapyrroles**; *often known also as* **porphin** *or* **porphine**. It consists of a ring of four pyrrole nuclei linked each to the next at their α positions (i.e. those adjacent to their nitrogen atoms) through a methine group, –CH= (*compare* **corrin**).



The structure is aromatic and tautomeric, two hydrogen atoms being associated with any two of its four nitrogen atoms (though for the purposes of nomenclature the name 'porphyrin' implies that the saturated nitrogen atoms are at positions 21 and 23 in the molecule unless there is a specific indication otherwise). Many di- or trivalent metal ions are chelated by porphyrin through these four central nitrogen

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atoms. [*Note*: It was recommended in 1986 that the widely used Fischer system of (incomplete) numeration for the porphyrin ring be discontinued in favour of one in which all the atoms are numbered, the C atoms 1 to 20 and the N atoms 21 to 24.] The systems for numbering tetrapyrrole carbons are shown at **bacteriochlorophyll**. Porphyrin itself is a synthetic substance, deep purple in colour. **2** any member of a large group of naturally occurring or synthetic derivatives or analogues of porphyrin (def. 1), of which **protoporphyrin IX** and its derivatives, especially the chlorophylls and hemes, are the most important.

porphyrinogen **1** 5,10,15,20,22,24-hexahydroporphyrin; *see* **porphyrin**. **2** *a general name for* the corresponding hexahydro derivative of any **porphyrin** (def. 2).

porphyrinuria the excretion of abnormally large amounts of porphyrins in the urine. *See also* **porphyria**.

porphyro+ *or (before a vowel)* **porphyr+** *comb. form* denoting purple.

porphyropsin a purple, light-sensitive, visual pigment in the rod cells of the retinas of freshwater and migratory fishes and some amphibians, consisting of a rod-type **opsin** combined (as a Schiff's base) with 3,4-didehydro-11-*cis*-retinal. It has an absorption maximum at ≈522 nm and is analogous in function to **rhodopsin** in other vertebrates.

portable *(in molecular biology)* describing DNA sequences that can be inserted into recombinant molecules for the purposes of gene expression; e.g. portable promoter, portable Shine–Dalgarno sequence, etc.

portal **1** relating to a blood vessel, or system of blood vessels, that carries blood from one capillary bed to another, especially the hepatic portal vein. **2** relating to a porta, such as the hepatic porta (porta hepatis). **3** the route of entry into the body of a drug, microorganism, beam of radiation, etc. (or sometimes of its exit therefrom).

porter any transporter of solutes between aqueous phases on either side of a lipid membrane. The term includes **antiporter**, **symporter**, and uniporter (*see* **uniport**).

Porter **1 George, Baron Porter** of Luddenham (1920–), British physical chemist; Nobel Laureate in Chemistry (1967) jointly with R. G. W. Norrish, the prize being shared with M. Eigen 'for their studies of extremely fast chemical reactions, effected by disturbing the equilibrium by means of very short pulses of energy'. **2 Rodney Robert** (1917–85), British biochemist and immunochemist noted particularly for his isolation of the constituent polypeptide chains of antibody molecules and for formulating the four-chain structure of such molecules; Nobel Laureate in Physiology or Medicine (1972) jointly with G. M. Edelman 'for their discoveries concerning the chemical structure of antibodies'.

positional cloning a strategy for the identification of a gene of unknown function responsible for a genetic disease. The phenotype is correlated with a chromosomal site, the DNA of that region is cloned and compared with that in normal individuals. If a single gene is involved, it is sequenced, and the protein structure deduced. An example is the discovery of the genetic basis of cystic fibrosis and the identification of the **cystic fibrosis transmembrane conductance regulator** (CFTR).

positional information information supplied to or possessed by cells according to their position in a multicellular organism.

positional isomer any of two or more constitutional isomers that differ in the position of a particular substituent or group.

positive **1** having a value greater than zero. **2** *(in mathematics)* of the same value but of opposite sense to that regarded as negative. **3** (of the results of a test) indicating the presence of the material or condition tested for. **4** (of an electric charge) having the opposite polarity to the charge of an electron. **5** (of a molecular entity) having a positive electric charge; having a deficiency of electrons. **6** (of a point in an electric circuit) having a higher potential than some other point to which a potential of zero is assigned. **7** *(in biology)* signifying growth or movement towards a (specified) stimulus. **8** *(in photography)* an exposed and developed photographic film, plate, or print showing an image in colours or tones corresponding to those of the object photographed. *Compare* **negative**. **—positiveness** *n.*; **positivity** *n.*

positive chromatography *(sometimes)* any method of purification of substances by affinity chromatography in which a substance of interest in a sample interacts with and is selectively retained by the adsorbent, especially as opposed to **negative chromatography**.

positive control the initiation or enhancement of some biological activity by the presence of a specific molecular entity.

positive cooperativity cooperative ligand binding in which binding of one ligand to one site on a macromolecule increases the affinity at other sites for the subsequent binding of the same or ligands.

positive correlation *see* **correlation** (def. 2).

positive effector *see* **effector**.

positive electron *an alternative name for* **positron**.

positive feedback *see* **feedback** (def. 1).

positive staining a technique used for preparing specimens for electron microscopic examination in which charged biological macromolecules or structures are rendered electron-dense by allowing heavy-metal ions of opposite charge to bind to them. *Compare* **negative-contrast technique**.

positron *or* **positive electron** *symbol*: β^+; an elementary particle that is the antiparticle of the electron. It has the same mass as an electron and a numerically equal but positive electric charge.

positron emission tomography *see* **tomography**.

post+ *or (sometimes)* **post-** *prefix* denoting after in time or sequence; behind, posterior to.

postabsorptive describing the period immediately after absorption of food.

posterior after in position, sequence, or time; behind; following.

posterior lobe the posterior lobe of the pituitary gland; i.e. the **neurohypophysis**.

postlysosome a degenerate **telolysosome** that has lost its enzymes.

postmitochondrial fraction *or* **postmitochondrial supernatant** *or* **supernatant fraction** *an operational term for* the part of a homogenate of eukaryotic cells or tissue remaining after sedimentation of the mitochondrial fraction by centrifugation. It consists essentially of the **microsomal fraction** and the cytosol.

post-mortem **1** occurring after death. **2** a post-mortem examination; necropsy, or **autopsy**.

postnatal describing the period after birth or giving birth.

postpartum describing the period immediately after birth or giving birth.

postprandial describing the period immediately after intake of food.

postreplication repair *see* **recombinational repair**, **mismatch repair**.

postreplicative describing the period following replication of a cell or of a nucleic-acid molecule.

postribosomal fraction *or* **postribosomal supernatant** *or* **supernatant fraction** *an operational term for* the part of a homogenate of eukaryotic cells or tissue remaining after sedimentation of the ribosomal (microsomal) fraction by centrifugation. It consists essentially of the cell sap.

postsynaptic **1** describing a neuron or a neuronal membrane that is on the efferent side of a synapse. **2** describing the membrane of a muscle cell at a motor end-plate.

postsynaptic membrane *see* **synapse**.

post-transcriptional describing any phenomenon or process occurring after completion of transcription of genomic nucleic acid. **—post-transcriptionally** *adv.*

post-translational describing any phenomenon or process occurring after completion of translation of messenger RNA into polypeptide; postsynthetic. **—post-translationally** *adv.*

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post-translational modification *or* **post-translational processing** any enzyme-catalysed change to a protein made after it is synthesized by the translation of messenger RNA. Examples are proteolytic cleavage, **glycosylation**, **methylation**, **phosphorylation**, and **prenylation**.

potash **1** *the common name for* potassium hydroxide or potassium carbonate. **2** *the name for* potassium in the common names of certain of its salts.

potassium *or (in scientific and medical Latin)* **kalium** *symbol*: K; a soft, silvery white, highly reactive, metallic element of group 1 of the (IUPAC) **periodic table**; atomic number 19; relative atomic mass 39.0983. Natural potassium is a mixture of stable nuclides of mass numbers 39 (93.2 atom percent) and 41 (6.7 atom percent) together with a minute proportion of the radionuclide of mass number 40 (0.012 atom percent). Potassium is widely distributed in all living organisms, besides occurring in various minerals; it is one of the most abundant elements of the Earth's crust. It forms a monovalent cation, K^+. Several artificial radioactive isotopes are known. In the body, potassium is a major intracellular cation, with little in the extracellular compartment; the range in normal human plasma is 3.6–5.0 mmol L^{-1}, with serum 0.2–0.3 mmol L^{-1} higher due to release from platelets on clotting. The cellular uptake of potassium is stimulated by insulin, and its excretion by the kidney is indirectly controlled by aldosterone, which stimulates sodium reabsorption in the distal tubules, potassium being excreted by passive transfer due to the electrochemical gradient thereby created. It is actively pumped into cells by **sodium/potassium-ATPase**. *See also* **hyperkalemia**, **hypokalemia**.

potassium-40 the naturally occurring radioactive nuclide $^{40}_{19}K$. It has a half-life of 1.28×10^9 years, emitting beta particles (i.e. electrons) of 1.34 MeV max. and gamma radiation of 1.46 MeV.

potassium-42 the artificial radioactive nuclide $^{42}_{19}K$. It has a half-life of 12.36 h, emitting high-energy beta particles (i.e. electrons) of 3.52 MeV max. (82%) and 1.97 MeV max. (18%), together with gamma radiation of 1.52 MeV (18%) and 0.31 MeV (0.15%).

potassium channel *or* **K^+ channel** any one of a number of types of structure that permit controlled (gated) passage of potassium ions, predominantly efflux, through membranes; these channels exhibit considerable diversity, but in excitable cells their role is to set the resting potential, participate in restoring it after depolarization, and attenuate and regulate potentials generated by other excitatory inputs. The main subdivisions of potassium ion channel are: (1) those primarily responding to membrane polarization, termed voltage-dependent, voltage-gated, or delayed rectifier (*see* **rectification**) K^+ channels; transmembrane (typically six transmembrane domains, designated S1 to S6) proteins; example, channel protein KV1.3 (human): database code CIK3_HUMAN, 523 amino acids (58.18 kDa); there are six motifs; (2) Ca^{2+}-activated K^+ channels, which are activated by increase of intracellular Ca^{2+} concentration; (3) receptor-coupled channels, which may be activated or inhibited by receptor occupancy; these themselves fall into two classes – those which have an intrinsic ion channel as part of the receptor, and those which act through a G-protein that activates an independent channel; example of the latter from human: database code IRK7_HUMAN, 423 amino acids (48.51 kDa); and (4) ATP-sensitive K^+ channels that close in response to increased intracellular ATP/ADP ratios generated by increased metabolic flux; example, heart K_{ATP} channel from human: database code IRK5_HUMAN, 419 amino acids (47.67 kDa). Types 3 and 4 are known as inward rectifier channels, in that they favour inward movement of K^+. Inward rectifier channels have two transmembrane domains rather than the six of voltage-gated channels. However, all K^+ channels have a loop known as the H5 or P region, which is thought to line the conducting pore. In voltage-gated channels, this lies between segments S5 and S6, and in inward rectifier channels between the two transmembrane domains.

potency *(in pharmacology)* an expression of the activity of a drug or other agent, in terms of either the concentration or the amount needed to produce a defined effect. It is an imprecise term that should always be further defined. *Compare* **EC_{50}**, **IC_{50}**.

potential *(in physics)* **1** the work done in bringing unit positive charge, unit positive pole, or unit mass from infinity to a specified point in an electric, magnetic, or gravitational field, respectively. **2 electric potential**. **3 electric potential difference**.

potential difference *abbr.*: p.d.; **1** generally, the difference in **potential** (def. 1) between any two points. **2** *see* **electric potential difference**.

potential divider a chain of resistors (or inductors or capacitors) connected in series, across which an electric potential may be applied and from which a desired fraction of the potential may then be obtained from a contact suitably placed in the chain. *See also* **potentiometer** (def. 3).

potential energy *abbr.*: PE; *symbol*: E_p *or* V *or* Φ; the energy of a body or system consequent upon its physical state or its position in an electric, magnetic, or gravitational field. It is expressed as the work necessary to bring it to its present state or position from a reference state or position, to which a potential energy value of zero is assigned.

potential energy barrier *or* **energy barrier** **1** the difference between the bond energy at which a molecule dissociates and the energy of that molecule in the ground state. **2** the difference between the energy of the ground state of an enzymically activated reaction complex and the sum of the energies of the ground states of the reactants forming the activated complex.

potential gradient the potential difference per unit distance between a point of higher and one of lower (electric) potential; the algebraic differential of this at a particular point.

potentiate to cause to be (more) potent, especially to increase the potency of a drug or other agent. —**potentiation** *n.*

potentiometer **1** a precision instrument for measuring an electric potential difference of constant polarity without drawing current from the circuit being examined. In its simplest form, it consists of a length of wire of uniform resistance and across which a constant potential is applied. By means of a sliding contact the proportion of this applied potential is found that will balance the potential being measured as determined by a null reading on a galvanometer. **2** a direct-reading electronic device for measuring electric potential difference or electromotive force without drawing appreciable current. **3** *or (informal)* **pot** a development of a potential divider consisting of a resistor with a movable contact and used, especially in electronics, either as a potential divider or as a variable resistor. —**potentiometry** *n.*; **potentiometric** *adj.*; **potentiometrically** *adv.*

potentiometric titration *or (sometimes)* **electrometric titration** titration in which an electrode reversible to one of the ionic components of the analyte or titrant is immersed in the analyte solution and the electric potential of the electrode (relative to that of an inert reference electrode) is measured during addition of titrant. Because the potential of an electrode is a logarithmic function of the activity of the ion to which the electrode is reversible, an abrupt change in its potential is observable as an equivalence point is approached.

potocytosis a mechanism for small molecule transport across eukaryotic cell membranes that uses **caveolae** rather than clathrin-coated pits.

Potter–Elvehjem homogenizer a device for preparing small quantities of cell or tissue homogenates. It consists of a cylindrical pestle (of glass, Perspex, or Teflon) that fits closely into a hard-glass test tube. Cells or small pieces of tissue in a suspending medium are placed in the tube and the pestle is rotated by means of an electric motor while the tube is slowly moved up and down by hand, a shear thereby being imparted to the contents of the tube. [After van Rensselaer Potter

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(1911–), US biochemist, and Conrad Arnold Elvehjem (1901–62).]

POU domain a feature found in many **transcription factors**. Its name derives from the fact that it was first recognized after comparison of cDNAs encoding three families of transcriptional regulators, Pit (*see* **PIT**), **Oct**, and Unc (*see*, e.g., **unc-86**). POU domain genes now also include the Brn family and others. The POU domain is a bipartite DNA-binding domain, i.e. it has two prominent protein domains that confer sequence-specific DNA binding. One of these domains is homologous to the domain found in other transcription factors and is called the POU homeodomain, whereas the other is specific to these factors and is called the POU-specific domain. The recognition sequences are A/T-rich, including the highly conserved **octamer** sequence 5′-ATGCAAAT-3′. The domain can also confer special protein–protein binding properties. Example i-POU (Pou inhibitory) protein of *Drosophila melanogaster*: database code IPOU_DROME, 367 amino acids (39.83 kDa).

pound *symbol*: lb; the avoirdupois unit of mass, now defined as 0.453 592 338 kg exactly.

powder pattern *or* **powder diagram** a diffraction pattern obtained from a specimen of a crystalline material in finely divided form. The specimen is rotated in a parallel beam of monochromatic X-rays, electrons, neutrons, etc. so that all planes of the crystals assume all possible orientations with respect to the incident beam.

power **1** *symbol*: *P*; a measure of the rate of doing work, expressed as energy divided by time. The derived SI unit of power is the **watt**. **2** *(in optics)* a measure of the ability of a lens or mirror to magnify, expressed as the reciprocal of the focal length of the lens or mirror in metres. **3** *(in mathematics)* **a** *an alternative name for* **exponent** or index; e.g. 2 to the power $3 = 2^3$). **b** one more than the cardinal number of times that a number or expression has to be multiplied by itself to give a required number; e.g. 2 to the power $3 = 2 \times 2 \times 2$. **c** one more than the ordinal number of times that a particular number has to be multipled by itself to give a required number; e.g. the third power of 2 is $8 = 2 \times 2 \times 2$.

poxvirus any member of the Poxviridae, a family of large, double-stranded DNA viruses, in class I of the **Baltimore classification**. They consist of a single molecule of DNA of 130–240 MDa together with 30 or more structural proteins, a number of viral enzymes, and lipid. Their hosts range from insects to mammals; examples include the viruses of variola (smallpox) and vaccinia (cowpox) – but not of varicella (chickenpox) – in humans, and the virus of myxomatosis in rabbits.

Pp *symbol for* the propionyl group.

PP *abbr. for* pancreatic polypeptide.

PP_i *symbol for* inorganic pyrophosphate.

P particle a liberated, mature **kappa particle**.

ppb *or* **p.p.b.** *abbr. for* parts per billion, i.e. parts per 10^9.

PP cell *or (formerly)* **F cell** a type of cell containing granules that store pancreatic polypeptide (**pancreatic hormone**). In adult humans such cells are located exclusively in the pancreas (79% in the islets, 19% in the acini, and 2% in the ducts).

pp[CH_2]pA *symbol for* adenosine 5′-[α,β-methylene]triphosphate; an analogue of ATP in which the α,β-bridging oxygen atom has been replaced by a methylene group.

PPF *or* **PP factor** *abbr. for* pellagra-preventative factor; an early name for **nicotinic acid** or **nicotinamide**.

ppGpp *symbol for* guanosine 3′-diphosphate 5′-diphosphate (*also known as* **magic spot I**). *See* ***relA***, ***spoT***.

PPIase *abbr. for* peptidylprolyl isomerase.

PPLO *abbr. for* pleuropneumonia-like organism (i.e. **mycoplasma**).

ppm *or* **p.p.m.** *abbr. for* parts per million, i.e. parts per 10^6.

PPO *abbr. for* 2,5-diphenyloxazole; a substance useful as a primary fluor in liquid scintillation counting.

pppGpp *symbol for* guanosine 3′-diphosphate 5′-triphosphate (*also known as* **magic spot II**). *See* ***relA***.

***PP*RibP** *symbol for* (5-)phospho(-α-D-)ribosyl diphosphate.

PPS *(in clinical chemistry) abbr. for* pepsin A.

ppt **1** *or* **ppt.**; *abbr. for* precipitate. **2** *or* **p.p.t.** *abbr. for* parts per trillion, i.e. parts per 10^{12}.

PPT *abbr. for* preprotachykinin (*see* **protachykinin β precursor**, **tachykinin**).

PQ *abbr. for* plastoquinone.

PQH_2 *abbr. for* dihydroplastoquinone (i.e. **plastoquinol**).

PQQ *abbr. for* pyrroloquinoline quinone (i.e. **methoxatin**).

Pr *symbol for* **1** praseodymium. **2** the propyl group.

Pr^i *symbol for* the isopropyl group, $(CH_3)_2CH$–.

prazosin *or* **furazosin** a quinazoline antagonist of α_1 adrenoceptors; it has anti-hypertensive properties.

pre+ *or* **pre-** *prefix* **1** before in time, position, sequence, rank, etc.; *compare* **pro+** (def. 1). **2** denoting a substance that moves faster (or further) than a specified substance in a separative procedure (e.g. prealbumin). Usage in this sense for naming proteins is now deprecated in order to avoid confusion with def. 3. **3** denoting a (usually metabolic) precursor, whether endogenous (e.g. prehormone, prekallikrein, pre-messenger RNA, preprotein, pretyrosine) or exogenous (e.g. precarcinogen), of the (class of) substance specified; *Compare* **pro+** (def. 3); *see also* **prepro+**.

PRE *abbr. for* proton relaxation enhancement.

prealbumin *an operational (and confusing) term for* either of two protein-containing zones observed to migrate more rapidly towards the anode than does serum albumin on zone electrophoresis of serum at pH 8.6 by some techniques. The faster-moving of these zones is now known to be **transthyretin** and the other to be acidic α_1-glycoprotein (i.e. **orosomucoid**).

prebiotic of or relating to the period before the appearance of living organisms on Earth.

precancerous describing a tissue or condition that is not yet malignant but is expected to form a cancer.

precarcinogen *(sometimes)* a chemical carcinogen that can be converted by metabolism into another of no less potency. *Compare* **proximate carcinogen**.

precarcinomatous describing a tissue that is expected to form a **carcinoma**.

P receptor *see* **purinoceptor**.

precerebellin a cerebellum-specific protein containing a 16-residue peptide known as cerebellin, flanked by Val-Arg and Glu-Pro. Precerebellin is the precursor of cerebellin, which is a protein of the postsynaptic structures of Purkinje cells. Concentrations of cerebellin are low at birth and (in humans) peak at days 5–15. It has a conserved sequence in mammals and birds. Example from human: database code CERB_HUMAN, 193 amino acids (21.07 kDa).

precess to undergo, or cause to undergo, **precession**.

precession (slow) gyration of the axis of rotation of a spinning body caused by application of a torque such that the axis of rotation generates a cone.

precipitant an agent or a reagent that induces the formation of a precipitate.

precipitate **1** to (cause to) come out of solution or suspension. **2** substance or material that is precipitated. —**precipitation** *n.*

precipitating antibody *an alternative name for* **precipitin**.

precipitin *or* **precipitating antibody** an antibody that is capable of reacting with a soluble antigen with the formation of an insoluble antigen–antibody complex.

precipitin reaction the reaction together of antigen and antibody near their equivalence point to form a cross-linked precipitate. Quantitative analysis of this interaction gives both the antibody content of an immune serum and an indication of the valency of the antigen. If the reaction occurs in a gel then the reactants form precipitin arcs.

precision-bore (of tubing or a tubular object) having a lumen whose diameter varies only within extremely narrow limits.

prednisolone 1,4-pregnadiene-11β,17α,21-triol-3,20-dione; a semisynthetic steroid with glucocorticoid action. *Compare* **prednisone**.

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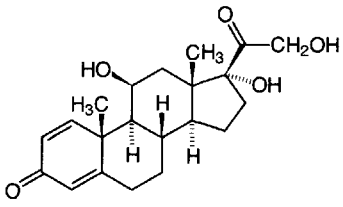
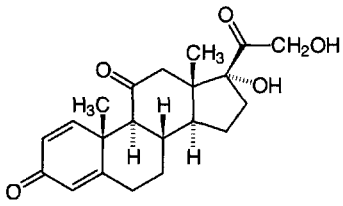


prednisolone

prednisone 1,4-pregnadiene-17α,21-diol-3,11,20-trione; a synthetic steroid with glucocorticoid action. *Compare* **prednisolone**.



preelectrophoresis a preliminary treatment of an electrophoresis gel in which a potential difference is applied in order to remove undesirable substances such as excess polymerization reagents.

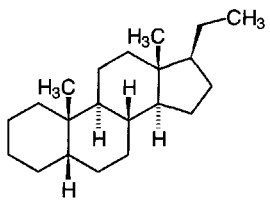
preflashing the hypersensitization of photographic emulsion by a preliminary exposure to a brief (≈1 ms) flash of light in order to increase its sensitivity to low levels of radiation and to render its response more nearly linear. It is useful especially in fluorography and (auto)radiography.

Pregl, Fritz (1869–1930), Austrian chemist; Nobel Laureate in Chemistry (1923) 'for his invention of the method of microanalysis of organic substances'.

pregnancy-associated α2-glycoprotein *see* **pregnancy zone protein**.

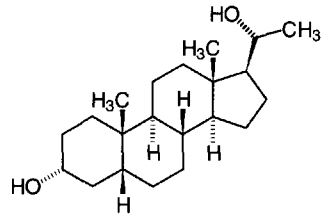
pregnancy zone protein *abbr.*: PZP; *other names*: pregnancy-associated α_2-glycoprotein; α_2-pregnoglobulin; a homotetrameric disulfide-linked proteinase inhibitor of the α_2-macroglobulin family that inhibits all four classes of proteinase by a 'bait-and-trapping' mechanism (*see* **bait region**). One of the major human pregnancy-associated plasma proteins, it may reach levels of 1.0–1.4 g L^{-1} just before term. It has extensive homology with human α_2-macroglobulin. In the sequence (example below) amino acids 1–24 form the signal, 26–1482 are the pregnancy zone protein, and 685–735 the bait region. Example (precursor) from human: database code PZP_HUMAN, 1482 amino acids (163.65 kDa).

pregnane a C_{21} steroid to which **pregnanediol** is related.



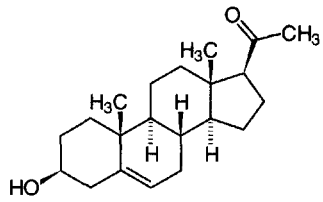
5β-pregnane

pregnanediol *a common name for* the steroid 5β-pregnane-3α,20α-diol; (20*S*)-5β-pregnane-3α,20-diol; the principal urinary metabolite of progesterone, occurring mainly as its 3-glucuronide. Its level in the urine increases during the luteal phase of the menstrual cycle and especially in the latter part of pregnancy, the excretion rate being a convenient (if approximate) index of the functional state of the corpus luteum and placenta.



pregnant mares' serum gonadotropin *abbr.*: PMSG; a clinically useful impure gonadotropin preparation extracted from the serum of pregnant mares – such serum has high activities of both follicle-stimulating hormone and luteinizing hormone. *Compare* **urogonadotropin**.

pregnenolone *a common name for* the steroid Δ^5-pregnen-3β-ol-20-one; 3β-hydroxypregn-5-en-20-one; a key intermediate on the biosynthetic route from cholesterol to progesterone. It has glucocorticoid activity and has been used in the treatment of rheumatoid arthritis. It is the product of **cholesterol monooxygenase (side-chain-cleaving)**.



α2-pregnoglobulin *see* **pregnancy zone protein**.

preincubate to bring a reaction mixture or a cell or tissue preparation to (chemical, metabolic, thermal, etc.) equilibrium before starting the reaction to be investigated. —**preincubation** *n.*

prekallikrein a plasma glycoprotein of 88 kDa (bovine), and a **blood coagulation** factor. It is the precursor of the proteinase **kallikrein**, to which it is converted by the action of factor XIIa. The protein contains four **apple domains**. The active site contains His, Asp, and Ser residues characteristic of a **charge-relay system**. Example from human (precursor): database code KAL_HUMAN, 638 amino acids (71.37 kDa).

Prelog, Vladimir (1906–98), Bosnian-born Swiss organic chemist and stereochemist; Nobel Laureate in Chemistry (1975) 'for his research into the stereochemistry of organic molecules and reactions' [prize shared with J. W. Cornforth].

prelysosomal vacuole *or* **prelysosome** *a former name for* **endosome** (def. 1).

pre-messenger RNA *abbr.*: pre-mRNA; the class of primary gene transcripts from which the corresponding messenger RNA molecules are subsequently formed by post-transcriptional processing; any member of this class. It comprises a substantial part of **heterogeneous nuclear RNA**.

pre-mRNA *abbr. for* pre-messenger RNA.

pre-mRNA processing protein (*abbr.*: PRP protein) *or* **pre-mRNA splicing factor** any of the proteins involved in processing the primary transcript RNA. Many of them function as components of a **spliceosome**. Most are components of snRNP particles, which are numbered U1, U2, etc; these proteins are

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usually numbered PRP2, etc.; the examples given are from yeast (*Saccharomyces cerevisiae*) unless stated to the contrary. PRP2 is an ATP-binding RNA helicase required for the first cleavage ligation reaction: database code PR02_YEAST, 876 amino acids (99.70 kDa). PRP5 is an ATP-binding RNA helicase required for unwinding of pre-mRNA and is part of the spliceosome, a so-called **DEAD-box** helicase: database code PR05_YEAST, 849 amino acids (96.25 kDa). PRP6: database code PRP6_YEAST, 899 amino acids (104.11 kDa). PRP8 is a U5 snRNP protein: database code PR08_YEAST, 2413 amino acids (279.18 kDa). PRP9 is required for U2 snRNP to bind to pre-mRNA: database code PR09_YEAST, 530 amino acids (62.96 kDa). PRP15 is an RNA-dependent ATPase required for branch-point recognition. PRP16 is an RNA helicase (another DEAD-box helicase): database code PR16_YEAST, 1071 amino acids (121.51 kDa). PRP18 is a component of the U4/U5/U6 snRNP; a homodimer: database code PR18_YEAST, 251 amino acids (28.35 kDa). PRP19 is a U2-binding protein of unknown function: database code PR19_YEAST, 502 amino acids (56.41 kDa). PRP21 is probably involved in retention of pre-mRNA in the nucleus: database code PR21_YEAST, 280 amino acids (33.02 kDa); PRP21 is a DEAD-box helicase involved in release of spliced mRNA from the spliceosome: database code PR22_YEAST, 1145 amino acids (129.86 kDa). PRP28 is a DEAD-box helicase involved in U4/U5/U6 SNRP; database code PR28_YEAST, 588 amino acids (66.62 kDa). PRP38 is involved in maintenance of U6 snRNA: database code PR38_YEAST, 242 amino acids (27.94 kDa). PRP39 facilitates interaction between U1 snRNP and the 5′-splice site: database code PR39_YEAST, 629 amino acids (74.55 kDa).

premurein-leader peptidase EC 3.4.99.35; *other names*: prolipoprotein-signal peptidase; signal peptidase II; SPase II. An enzyme that cleaves a single bond between Gly^{20} and alkylated Cys^{21} in a bacterial lipoprotein, detaching the leader peptide. Example from *Escherichia coli*: database code LSPA_ECOLI, 164 amino acids (18.14 kDa).

prenol *the recommended name for* any **isoprenoid** of general formula $H–[CH_2–C(CH_3)=CH–CH_2–]_n–OH$; i.e. any primary monohydroxy alcohol whose carbon skeleton consists of two or more isoprene residues linked head to tail. *See also* **polyprenol**.

prenyl the univalent alkyl group derived from a **prenol** by loss of its hydroxyl group. *See also* **polyprenyl**. *Compare* **isopentenyl**.

prenylation the enzymic addition of **prenyl** moieties to proteins as a post-translational modification; **geranyl**, **farnesyl**, or **geranylgeranyl** groups may be added. The process involves reaction of a prenyl diphosphate with a cysteinyl sulfhydryl group near the C terminus of the protein, to give a prenyl–S–Cys moiety. Characteristically a Cys-ali-ali-Xaa sequence is recognized by the transferase that mediates the reaction, where Cys is cysteine, ali is an aliphatic amino acid, and Xaa is any amino acid. When Xaa is serine, alanine, or methionine the protein is farnesylated; when Xaa is leucine it is geranylgeranylated, but this is variable; for example, in the case of Rab 3A (*see* ***RAB***), the Cys-Xaa-Cys motif leads to geranylgeranylation on both cysteine residues and methyl esterification of the terminal carboxyl, while in other members of the Rab family Cys-Cys directs geranylgeranylation without esterification. The function of the process appears often to be regulation of protein–protein and protein–membrane interaction.

prenyltransferase *see* **dimethylallyl*trans*transferase**.

PR-enzyme *an old name for* **1 phosphorylase phosphatase** (EC 3.1.3.17). [PR stood originally for prosthetic-group removing, later for phosphorylase rupturing, and later still for phosphate removing.] **2** deoxyribodipyrimidine photo-lyase (EC 4.1.99.3). [PR stood for photoreactivating.]

preparative ultracentrifuge any ultracentrifuge designed for preparation or purification of tangible quantities of macromolecular substances, subcellular fractions, etc.

pre-part *or* **pre-peptide** *an alternative name for* **signal peptide**.

prephenate *a trivial name for* 2-oxo-3(1-carboxylato-4-hydroxy-2,5-cyclohexadiene-1)-propanoate; a nonaromatic intermediate in the branched biosynthetic pathway (the **prephenate pathway**) from chorismate to phenylalanine or tyrosine in most autotrophic organisms. *See also* **arogenate**.

prephenate dehydratase EC 4.2.1.51; *systematic name*: prephenate hydro-lyase (decarboxylating); an enzyme that catalyses the formation of phenylpyruvate from prephenate with release of H_2O and CO_2. This is a reaction in one of the pathways for the biosynthesis of phenylalanine. Example from *Bacillus subtilis*: database code PHEA_BACSU, 285 amino acids (31.86 kDa). In other cases (e.g. *Escherichia coli*) the activity is one domain of a bifunctional enzyme that also contains **chorismate mutase** (another enzyme of the phenylalanine biosynthetic pathway). Example from *E. coli*: database code PHEA_ECOLI, 386 amino acids (43.06 kDa). The mutase domain is in the N-terminal part of the database code, the dehydratase in the C-terminal part. *See also* **arogenate**.

prephenate dehydrogenase any of several enzymes that convert prephenate to 4-hydroxyphenylpyruvate with release of CO_2 and reduction of either NAD^+ or $NADP^+$. They function at a branch point in the pathway for the biosynthesis of aromatic amino acids, at which they initiate the branch of the pathway leading to tyrosine biosynthesis. They include prephenate dehydrogenase, EC 1.3.1.12; *systematic name*: prephenate:NAD^+ oxidoreductase (decarboxylating); *other name*: hydroxyphenylpyruvate synthase; an enzyme that also has **chorismate mutase** activity, so can convert chorismate to hydroxyphenylpyruvate. Example from *Escherichia coli*: database code TYRA_ECOLI, 373 amino acids (42.04 kDa). There is also prephenate dehydrogenase ($NADP^+$), EC 1.3.1.13; *systematic name*: prephenate:$NADP^+$ oxidoreductase (decarboxylating). Example from *Saccharomyces cerevisiae*: TYR1_YEAST, 452 amino acids (50.92 kDa).

prephenate pathway a pathway for the synthesis of phenylalanine and tyrosine from chorismate, utilizing prephenate as an intermediate. Prephenate is formed from chorismate by **chorismate mutase**. It is converted by **prephenate dehydrogenase** to 4-hydroxyphenylpyruvate, from which tyrosine is formed by transamination with glutamate as the amino-group donor. For the synthesis of phenylalanine, phenylpyruvate is formed by **prephenate dehydratase**, and is then converted to phenylalanine by transamination, glutamate again acting as amino-group donor. *See also* **arogenate**.

pre-piece *an alternative name for* **signal peptide**.

prepolypeptide *or* **presecretory polypeptide** the transient, primary translation product of a eukaryotic messenger RNA for any polypeptide destined to be secreted by a cell, irrespective of whether or not an intermediary **propolypeptide** is formed; the polypeptide counterpart of **preprotein**. *See also* **prepropolypeptide**.

prepro+ *or* **prepro-** *compound prefix* denoting preprotein of the proprotein of a specified protein, or prepolypeptide of the propolypeptide of a polypeptide.

preprocessing *a fanciful name for* enzymic conversion of a preproprotein (or prepropolypeptide) to a proprotein (or propolypeptide).

preprohormone the prehormone of any prohormone of a protein or (poly)peptide hormone. Examples are: preproglucagon, preproinsulin, preproparathyrin, prepro-VIP.

preprophase band a dense band of microtubules, 1–3 μm wide, that appears just beneath the cell membrane before the start of cell division in the cells of higher plants. It precedes the onset of prophase and then disappears as mitosis begins, yet it somehow determines the plane of orientation of the new cell plate forming in late telophase and marks the zone of the parental cell wall where fusion with the growing cell plate ultimately occurs.

prepropolypeptide the prepolypeptide of any propolypeptide. Examples are: preproenkephalin and prepromelittin.

preproprotein the preprotein of any proprotein. Examples

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are: preproalbumin (serum) and prepro-von Willebrand factor. Note that preprolactin is not a preproprotein since prolactin is not a proprotein.

preprotachykinin *abbr.*: PPT; *see* **protachykinin β precursor.**

preprotein the transient, primary translation product of a eukaryotic messenger RNA for any protein destined to be secreted by a cell, irrespective of whether or not an intermediary **proprotein** is formed. It is detectable only in a cell-free protein-synthesis system since in an intact cell its N-terminal presequence (i.e. **signal peptide**) is cleaved off before translation has been completed. *See also* **prepolypeptide**, **preproprotein.**

presecretory polypeptide *an alternative name for* **prepolypeptide.**

presequence *an alternative name for* **1 signal peptide. 2** transport sequence (of a protein imported into mitochondria), especially in those instances where the sequence is not removed by proteolytic cleavage prior to translocation through the membrane but is removed at its final destination.

pressor *(in physiology)* **1** of, relating to, or bringing about an increase in arterial blood pressure. **2** any drug or other agent that has a pressor effect.

pressure *symbol*: *p or P*; the force per unit area acting on a surface; i.e. $p = F/A$. The pressure at a point in a fluid is equal to the force per unit area on an infinitesimal plane situated at that point, and in a fluid at rest it is the same in all directions. The SI derived unit of pressure is the **pascal**; the **bar** is also acceptable (*see* **standard atmosphere**). *See also* **millimetre of mercury**, **torr.**

pressure dialysis dialysis in which a hydrostatic pressure is applied to the material being dialysed in order to minimize its initial dilution by solvent entering by osmosis.

pressure homogenization *or* **nitrogen cavitation** a method of disrupting cells that depends on equilibrating a cell suspension with a gas, e.g. nitrogen, at high pressure (up to 7 MPa) and then suddenly reducing the pressure, whereupon the gas dissolved in the cytoplasm is explosively released.

pressure-jump method a relaxation technique in which change of pressure is the disturbing factor. *See* **relaxation kinetics.**

pre-steady-state kinetics *or* **transient-phase kinetics** the kinetics of a catalysed reaction during the phase in which the concentration of the catalyst–reactant complex rises from zero to its steady-state value. For an enzyme-catalysed reaction this phase usually occupies a very brief period of time (from a second to a microsecond or less) and special techniques are required for its study. *See also* **rapid reaction kinetics.**

pre-swollen describing a commercial gel preparation that has already been equilibrated with water or another liquid phase.

presynaptic **1** *(in anatomy)* **a** designating a neuron that transmits an impulse directly to a synapse. **b** of or pertaining to that part of such a neuron close to the synapse. **2** *(in cytology)* prior to meiotic **synapsis.**

presynaptic membrane *see* **synapse.**

presynaptic nerve ending *see* **synapse.**

pre-transfer RNA *abbr.*: pre-tRNA; the class of primary gene transcripts from which the corresponding transfer RNA molecules are subsequently formed by post-transcriptional processing; any member of this class.

pretransition temperature the specific temperature at which a lipid bilayer being heated shows the first signs of **melting** (def. 2), before it reaches its transition temperature. Special techniques (e.g. employing spin-labelled or fluorescent probes) are required for its detection and study.

pretyrosine *an obsolete name for* **arogenate.**

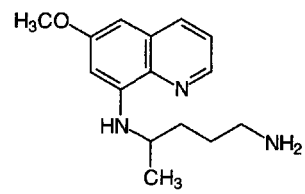
previtamin *a less common word for* **provitamin.**

Pribnow box a promoter site in *Escherichia coli* and phage genes that specifically binds **RNA polymerase.** The Pribnow box has the consensus sequence TATAAT and is centred at –10 (ten nucleotides on the 5′ side of the first nucleotide transcribed, which is designated +1).

PRibPP *symbol for* (5-)phospho(-α-D-)ribosyl diphosphate.

primaeval soup *a variant spelling of* primeval soup; *see* **primordial soup.**

primaquine one of several 8-aminoquinoline antimalarial drugs. It is active against the exo-erythrocytic form of the parasite, and can effect radical cures as well as serving as a preventive medicine.



primary *(in chemistry)* **1 a** describing an alkyl compound (e.g. an alkanol) in which the functional group (e.g. a hydroxyl group) is attached to a carbon atom linked to only one other. **b** describing the carbon atom bearing the functional group in such a compound. **2** describing an amide or an amine in which a single appropriate group is attached to a nitrogen atom. **3** describing a salt formed by replacing only one of the ionizable hydrogen atoms of a tribasic acid by another cation. *Compare* **secondary**, **tertiary.**

primary cell wall the outer layer of the wall of a plant cell. It is produced by deposition of cellulose microfibrils against the cell plate separating two daughter cells newly formed by division. When cell extension is complete, it is supplemented by deposition of the secondary cell wall (*see* **secondary cell wall deposition**).

primary culture a culture of cells (or tissue) that have been obtained directly from their place of origin.

primary electron an electron incident on a surface that causes **secondary electrons** to be emitted.

primary F′-containing strain *see* **F′ plasmid.**

primary fluor *or* **primary scintillator** *or* **primary solute** *(in liquid scintillation counting)* the fluorescent substance to which radiation energy is directly tranferred from excited molecules of the solvent. *Compare* **secondary fluor.**

primary granule *an alternative name for* **azurophil granule.**

primary hormone *a term proposed to embrace* any hormone that acts rapidly and uses a cyclic nucleotide as second messenger.

primary immune response the response produced in an animal when it is first exposed to an antigen. It consists characteristically of a slow production of antibody molecules and the priming of lymphoid tissue in readiness for the production of a **secondary immune response** on subsequent challenge with the same antigen.

primary kinetic isotope effect an **isotope effect** on a reaction rate that is attributable to isotopic substitution of an atom to which a bond is made or broken in the rate-limiting step or in a pre-equilibrium step of a specified reaction.

primary lysosome *or* **protolysosome** a **lysosome** containing newly synthesized acid hydrolases that have not as yet reacted with their ultimate substrates. A primary lysosome may be considered as a vesicle for transport between the site of enzyme synthesis and the digestive body or **secondary lysosome.**

primary metabolism the ensemble of metabolic activities that are common to most if not all living cells and are necessary for growth, maintenance, and survival. *Compare* **secondary metabolism.**

primary metabolite any intermediate in, or product of, **primary metabolism.**

primary response *see* **primary immune response.**

primary scintillator *an alternative name for* **primary fluor.**

primary solute *an alternative name for* **primary fluor.**

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primary solvent *(in liquid scintillation counting using mixed solvents)* the solvent to which energy of the radiation emitted by the specimen is first transferred as excitation energy.

primary standard **1** any standard of measurement of nationally or internationally agreed and specified value that is used as the basis of a unit of measurement. **2** a specimen of a particular substance that is of extremely high purity and stability and that serves as an ultimate reference to which may be compared the purity of any secondary standard used in analysis.

primary structure the first order of complexity of structural organization exhibited by polypeptide and protein molecules and by polynucleotide and nucleic-acid molecules. When applied to a segment of a polypeptide chain or to a polypeptide or protein molecule, it refers to the linear sequence of the amino-acid residues of the polypeptide chain(s) without regard to spatial arrangement apart from configuration at the α-carbon atoms (and excluding the positions of any disulfide bonds). When applied to a segment of a polynucleotide chain or to a polynucleotide or nucleic-acid molecule, it refers to the linear sequence of the nucleotide residues of the polynucleotide chain(s) without regard to spatial arrangement. *Compare* **secondary structure**, **tertiary structure**, **quaternary structure**.

primary transcript the RNA as synthesized by RNA polymerase directly from a gene, unaltered by any further modification, such as **splicing**, that it may undergo.

primase **1** any RNA polymerase that synthesizes an RNA primer needed for the initiation of DNA synthesis. Such enzymes vary greatly in structure, specificity, and mode of regulation. **2** *or* **DNA primase** the DNA-directed **RNA polymerase** (EC 2.7.7.–) of the bacterial **primosome**. In *Escherichia coli*, primase is the product of the *dnaG* gene while in T4 phage the primase is the product of gene 61. In either case, the primase is only active in the presence of other proteins which create a complex called a **primosome**. The complex participates in the unwinding of parental DNA strands ahead of the replication fork, and synthesizes short RNA primers for the **Okazaki fragments**. Example from *E. coli*: database code PRIM_ECOLI, 581 amino acids (65.49 kDa).

primate any member of the Primates, an order of placental mammals. Primates are characterized by flexible pentadactyl limbs, opposable first digits, good stereoscopic vision, and, in the higher apes, highly developed brains. Included are lemurs, tarsiers, monkeys, apes, and humans.

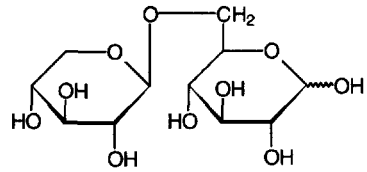
prime **1** the printer's character, ′, used (singly, doubly, etc.) as a mark to discriminate between characters or symbols representing things that are or would otherwise be indistinguishable. In chemical nomenclature it is used to distinguish between (1) identical locants referring to different moieties of the same molecule; or (2) two or more unspecified but differing univalent groups represented by the same symbol R. In physical chemistry it is used to differentiate the symbol for a quantity measured under arbitrary conditions from that for the corresponding quantity referred to the (thermodynamic) standard state; e.g. K', apparent equilibrium constant, from K, thermodynamic equilibrium constant; E_o', standard redox potential at a specified pH, from E_o, standard redox potential at a hydron activity of unity. **2** *(in biochemistry)* to provide a metabolic reaction with a primer; to bring about activation of a process or substrate. **3** *(in immunology)* to induce a **primary immune response** in an animal; to activate a cell specifically with respect to a given antigen. **4** *(in mathematics)* **a** having no other integral factor than itself and one. **b** **prime number**.

prime number any integer that possesses no integral factors and hence is divisible only by itself and 1.

primer **1** something used to **prime** (def. 2, 3). **2** an oligonucleotide required as the starting point for the stepwise synthesis of a polynucleotide from mononucleotides by the action of a nucleotidyltransferase. **3** a short-chain fatty acyl-CoA, e.g. acetyl-CoA or butyryl-CoA, required for the initiation of the stepwise enzymic synthesis, from two-carbon units, of long-chain fatty acids as their CoA derivatives. *See also* **glycogenin**.

primeval soup *or (esp. Brit.)* **primaeval soup** *an alternative name for* **primordial soup**.

primeverose 6-*O*-β-D-xylosyl-D-glucose; a disaccharide occurring in **madder**.



primordia *the plural of* **primordium**.

primordial existing at or from the beginning, primeval; earliest formed, primitive.

primordial soup *or* **primordial slime** *or* **primeval soup** *or (esp. Brit.)* **primaeval soup** the aqueous solution of organic compounds that is considered to have been the environment in which the synthesis of macromolecules first occurred and cellular life originated. *See also* **coacervate droplet**.

primordium (*pl.* **primordia**) an organ or part at the earliest stage of its development; a rudiment.

primosome a protein complex that is essential for the activity of the **primase** responsible for the synthesis of RNA primers in the replication of DNA in *Escherichia coli*. *See* **replication complex, replication of DNA**.

PRINTS a computer database of protein sequence motifs (**signatures**) used in the compilation of this dictionary and elsewhere to identify amino-acid sequences (typically sequences of about 10 residues) defining structural and functional features of protein sequences. *See also* **Appendix E**.

prion a term originally introduced to emphasize the proteinaceous and infective nature of the pathogen responsible for transmissible encephalopathies. These include **scrapie**, **kuru**, **bovine spongiform encephalopathy**, **Creutzfeld–Jakob disease**, **fatal familial insomnia**, and **Gerstmann–Sträussler syndrome**. The agent is now widely accepted to be a variant of the normal **prion protein**; it is believed that the variant folds abnormally and induces the normal protein also to fold abnormally, typically into beta configurations, which form aggregates. A similar phenomenon has been observed in yeast, hence the term 'yeast prion'. *See also* **virino**.

prion protein *abbr.*: PrP^C; a membrane protein of 33–35 kDa that is encoded in the mammalian genome; it contains, in humans, 253 amino-acid residues (near the same number in other species) and has a glycosylinositol phospholipid anchor. A variant, termed PrP^{Sc}, with the same amino-acid sequence, is found in the brains of sheep and other mammals affected by **spongiform encephalopathy**. PrP^C is rich in α helix but devoid of β sheet, while PrP^{Sc} contains much β sheet. PrP^{Sc} associates to form aggregates ('rods') in the central nervous system; these aggregates are seen in many manifestations of susceptibility to spongiform encephalopathy. Such mutations appear to be important in respect of the susceptibility of spongiform encephalopathy. Polymorphism, e.g. at position 171, occurs in several species and in subgroups in one species. Example: database code PRIO_SHEEP, 256 amino acids (27.88 kDa); eight motifs.

prism **1** any polyhedron of which two faces are polygons in parallel planes and the other faces are parallelograms. **2** a crystal form of which three or more faces are parallel to one axis. **3** a solid, bounded in part by two nonparallel plane faces and made of material transparent in the relevant region of the spectrum, that is used in optics to invert an image or to disperse or deviate a beam of light.

PRL *abbr. for* prolactin.

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pro+ *or* **pro-** *prefix* **1** before in time or position; anterior; projecting; *compare* **pre+** (def. 1). **2** for, on behalf of, substituting for, favouring, encouraging, etc. **3** *(in biochemistry)* denoting (inactive or less active) biosynthetic precursor of the (class of) proteinaceous agent specified, to which it is convertible by proteolytic cleavage in a specific manner. Examples are: proalbumin, prohormone, proinsulin, proprotein, and prothrombin (but not prolactin!). *Compare* **pre+** (def. 3). *See also* **+gen**.

Pro *symbol for* a residue of the α-amino (strictly, cyclic α-alkylamino) acid L-proline (alternative to P).

pro- *prefix* in symbols designating prochirality; *see* ***pro-R/pro-S* convention**.

proaccelerin *an alternative name for* factor V; *see* **blood coagulation**.

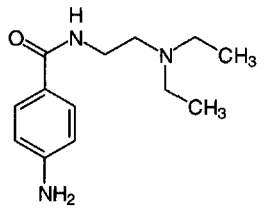
probability *(in statistics) symbol*: *p or P*; a measure of the likelihood of the occurrence of a given event, expressed as the ratio of the number of times it occurs in a series of observations to the total number of observations, or as its decimal equivalent.

probable error an older measure of sampling variability such that one-half of the events, observations, etc. in a **normal distribution** lie between the mean value minus the probable error and the mean value plus the probable error. The probable error is equal to the standard error multiplied by 0.6745.

proband *an alternative term for* **propositus**.

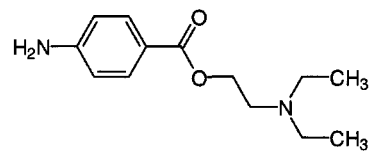
probe **1** something that searches into, examines, or tests; e.g. an instrument or tube used for exploring a cavity or sampling a fluid, or an electric conductor introduced into an electric circuit or a cavity resonator to provide electric coupling to an external circuit. **2** *(in biochemistry)* a chemical species, or a chemical group attached to a carrier molecule, used to investigate the chemical nature of some other particular chemical species or the physical nature of a particular environment, especially within an intact cell; a **reporter group**. Typically some measurable physical property of the probe (e.g. fluorescence, electron spin resonance) alters in a way that can be correlated with changes in the environment or in the macromolecule. Examples are a group having paramagnetic properties, for detection using electron spin resonance (*see*, e.g., **TEMPO**), and a fluorescent lipid molecule used to report membrane fluidity (*see*, e.g., **parinaric acid**). **3** *(in molecular biology) or* **gene probe** *or* **hybridization probe** an oligo- or polynucleotide that is complementary to an oligonucleotide or nucleic-acid sequence under investigation. The probe is normally labelled in a way that permits its ready detection, e.g. with a radioactive isotope or a fluorescent constituent. Hybridization of the probe to the oligonucleotide sequence under investigation allows that sequence to be detected. The technique finds much use in screening gene libraries, detecting oligonucleotides on blots of electrophoresis gels, and in other associated technologies. **4** to examine with or as with a probe.

procainamide a local anaesthetic similar in action to **procaine** but having a less easily hydrolysed amide linkage, which gives it longer duration of action.



procainamide azide a local anaesthetic; it binds the 43 kDa postsynaptic protein (μ chain *or* rapsyn) of the nicotinic **cholinoceptor** and is useful as a photoaffinity label.

procaine *or* **novocaine** the prototype injectable local anaesthetic. It brings about changes in the physical properties of the lipid bilayer towards a more fluid state, decreasing ordering of the fatty-acyl side chains.



procapsid a precursor of the virion of certain viruses, consisting of a viral capsid without its specific nucleic acid.

procarboxypeptidase component III a protein, resembling **elastase** but without enzyme activity, found in the pancreatic juice of ruminants in noncovalent association with zymogens, carboxypeptidse A, etc. It probably prevents denaturation of the latter in the acid of the duodenum. Example (bovine): database code CAC3_BOVIN, 240 amino acids (25.83 kDa).

procaryon *a variant spelling of* **prokaryon**.

procaryote *a variant spelling of* **prokaryote**.

process *(in anatomy)* a thin prominence or protuberance of a structure, or an extension or outgrowth of a cell.

processed gene a **pseudogene** that lacks the intervening sequence or sequences of the homologous functional gene. It usually contains a short segment consisting entirely or almost entirely of adenine nucleotides, attached near the 3′ end, and is thought to originate by reverse transcription of an mRNA template with incorporation of the cDNA so formed into genomic DNA. A processed gene is sometimes called a **retrogene**.

processing *(in molecular biology)* **covalent modification** either of the primary transcription product (i.e. RNA) of a DNA or of the primary translation product (i.e. polypeptide) of a messenger RNA. *See also* **post-translational modification**.

processive *(in molecular biology) or* **nondistributive** describing (the action of) any enzyme or catalytic complex that progressively synthesizes or degrades a biopolymer by effecting several or many cycles of the same type of reaction or reaction sequence without dissociating from the template or intermediate product (as appropriate) between catalytic events. *Compare* **distributive**.

processivity (of a nucleic acid polymerase) the average number of nucleotides inserted before the enzyme dissociates from its template. In the case of DNA polymerases, repair enzymes (such as Pol I in *Escherichia coli*) have low processivity replication enzymes (such as Pol II and its associated proteins in *E. coli*) have high processivity.

processosome a hypothetical ribonucleoprotein associated with processing of pre-RNA in the nucleolus.

prochiral describing a molecule, or a centre or axis in a molecule, that in itself is achiral but is capable of becoming **chiral** by a replacement reaction. In general, a prochiral molecule has a structure *Caabc*, where the '*a*' groups (or atoms) are identical. Replacement of one '*a*' by another group or atom, '*d*', leads to a chiral molecule. Thus, in ethanol, replacement of one ^{1}H of the methylene group by ^{2}H leads to a chiral structure which can be shown to be optically active. In a prochiral molecule *Caabc*, the chemically like '*a*' groups may be differentiated one from another in a reaction with a chiral molecule, especially an enzyme. An achiral molecule containing a double bond or a planar cyclic ring system is also prochiral if separate addition of an achiral reagent to each face leads to two enantiomeric products. *See also* ***meso*-carbon atom**, ***pro-R/pro-S* convention**. —**prochirality** *n.*

procholecystokinin precursor a member of the gastrin/cholecystokinin family, and a precursor for five different **cholecystokinins**. Example from human: database code CCKN_HUMAN, 115 amino acids (12.65 kDa).

Procion *the proprietary name for* a range of reactive dyes that includes Procion Blue H-B, Procion Red H-E3B, as well as a

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number of other dyes useful in biochemistry, especially in **dye-ligand chromatography**.

procoagulant *(sometimes)* any of factor V, factor VII, or factor VIII, each of which acts to accelerate the conversion of prothrombin to thrombin during **blood coagulation**.

procollagen a ≈150 kDa triple-helical protein that is an intermediate in the biosynthesis of **tropocollagen**, into which it is converted proteolytically by removal of the additional sequences at both the N and the C termini of each of the three peptide chains. Example, procollagen α1 (human): database code CA11_HUMAN, 1464 amino acids (138.73 kDa). *Compare* **protocollagen**.

procollagen *N*-endopeptidase EC 3.4.24.14; *other name*: procollagen *N*-proteinase; an enzyme that catalyses the cleavage of the *N*-propeptide of collagen chain α-1(I) at Pro-|-Gln and of chain α-2(II) at Ala-|-Gln.

procollagen-lysine 5-dioxygenase EC 1.14.11.4; *other names*: procollagen-lysine,2-oxoglutarate 5-dioxygenase; lysine hydroxylase; lysine,2-oxoglutarate 5-dioxygenase; an enzyme that catalyses the formation of hydroxylysine residues in collagen. The reaction is between dioxygen, procollagen L-lysine, and 2-oxoglutarate to form procollagen 5-hydroxy-L-lysine, succinate, and CO_2. Iron and **ascorbic acid** are cofactors. Example (precursor) from human: database code LYSH_HUMAN, 727 amino acids (83.49 kDa). *See also* **procollagen-proline dioxygenase**.

procollagen-proline dioxygenase EC 1.14.11.2; *systematic name*: procollagen-L-proline,2-oxoglutarate:oxygen oxidoreductase (4-hydroxylating); *other names*: proline,2-oxoglutarate-4-dioxygenase; protocollagen hydroxylase; proline hydroxylase; prolyl 4-hydroxylase. An enzyme converting L-proline into 4-hydroxy-L-proline; it catalyses a reaction between dioxygen, procollagen L-proline, and 2-oxoglutarate to form procollagen *trans*-4-hydroxy-L-proline, succinate and CO_2. Hydroxylation only occurs when proline is present in a polypeptide chain elongating on a ribosome. **Ascorbic acid** and Fe^{3+} are also required as cofactors, and the reaction is one of the few well-defined roles for ascorbic acid; it seems likely that scurvy, as a result of vitamin C deficiency, is due to defective activity of this enzyme, which plays a key role in collagen synthesis. The enzyme is a tetramer of two α chains and two β chains; the β chain is the multifunctional **protein disulfide isomerase** and hence has microsomal triacylglycerol transfer protein activity. Subcellular location is the endoplasmic reticulum lumen. There are two forms of α subunit, which are produced by alternative splicing of the same gene. Example from human (α precursor): database code P4HA_HUMAN, 534 amino acids (60.84 kDa). See also **procollagen-lysine 5-dioxygenase**.

proconvertin *an alternative name for* factor VII; *see* **blood coagulation**.

procorticotropin *or* **procortin** *an alternative name for* **proopiomelanocortin**.

procyclin *or* **PARP** a major surface antigen of procyclic forms of trypanosomes. It is GPI-anchored. Example B1-α precursor from *Trypanosoma brucei brucei*: database code PAR1_TRYBB, 143 amino acids (14.88 kDa).

prodrug a drug molecule that is itself inert but has pharmacological effects after **bioactivation**. An example is **ganciclovir**.

produce *(in mathematics)* to extend a line or a plane.

product **1** *(in biochemistry and chemistry)* something formed in a reaction. **2** *(in mathematics)* the result of multiplying together two or more numbers, quantities, or expressions.

product inhibition the inhibition of an enzymic reaction caused by increased concentration of one or more products of that reaction.

productive (capable of) yielding a product, result, or benefit.

productive binding *or* **eutopic binding** the binding of a substrate in a reactive mode at the active site of an enzyme. *Compare* **nonproductive binding**.

productive complex any enzyme–substrate complex in which the substrate is bound to the enzyme in a manner that renders catalysis possible so that products can be formed. *Compare* **abortive complex**.

productivity *(in biotechnology) symbol*: *r*; the mass of product formed per unit reactor volume per unit time; often per unit of enzyme or biomass. It is measured typically in kg m^{-3} h^{-1}.

proenkephalin a protein precursor for several neuropeptides including various **enkephalins** formed in brain and adrenal medulla. For example, in the human, proenkephalin A precursor yields four copies of [Met]enkephalin (100–104; 107–111; 136–140, 210–214) and single copies of each of [Leu]enkephalin (230–234), [Met]enkephalin–Arg–Gly–Leu (octapeptide) (186–193) and [Met]enkephalin–Arg–Phe (heptapeptide) (261–267), which arise by enzymatic cleavage of the gene product by cleavage at paired basic amino acids: database code PENK_HUMAN, 267 amino acids (30.79 kDa). Another human protein, proenkephalin B precursor (*other name*: β-neoendorphin–dynorphin precursor) yields single copies of α-neoendorphin, dynorphin, [Leu]enkephalin, rimorphin, and leumorphin, also by cleavage at paired basic amino acids: database code NDDB_HUMAN, 254 amino acids (28.38 kDa).

proenzyme *an alternative name for* **zymogen**.

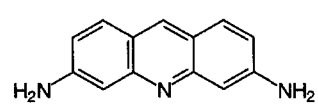
***pro-E*/*pro-Z* convention** if the two chemically-like hydrogen atoms of *ab*C=CH_2 are separately replaced by the achiral, *d*, an achirotopic stereogenic element is generated and two (diastereoisomeric) alkenes, *ab*C=CH*d* are fomed that are *E* and *Z* stereoisomers (*see* ***E*/*Z* convention**). The replacement has converted a prostereogenic element into which one which is stereogenic; the situation is comparable to the change, prochiral → chiral, although a chiral element is not involved. The two chemically-like hydrogen atoms are designated as *pro-E* and *pro-Z*, and are abbreviated as H_E and H_Z. Replacement of a *pro-E* hydrogen with ^2H yields an *E* diastereoisomer and the similar replacement of a *pro-Z* hydrogen yields the *Z* form. Example: the two hydrogen atoms of phospho*enol*pyruvate; that on the same side of the double bond as the COOH group is H_E, that on the same side as the OPO_3H_2 group is H_Z. Replacement of ^1H_E by ^2H yields (*E*)-[3-$^2H_1$]phospho*enol*pyruvate; the *Z* diastereoisomer results if ^1H_Z is replaced by ^2H. A similar situation is found in the side chain of **chorismic acid**.

proestrus *see* **estrous cycle**.

profibrinolysin *an alternative name for* **plasminogen**.

profilin a protein that *in vitro* prevents the polymerization of actin. In many cells it occurs as a 1:1 complex with monomeric actin, that appears to act as an intracellular storage form of actin. Profilin binds PtdInsP_2 and inhibits the γ isoform of phospholipase C (*see* **phospholipase**), an inhibition that is overcome when the enzyme is activated as a result of receptor kinase-dependent tyrosine phosphorylation. This activation appears in some way to recruit profilin–actin to the site of filament assembly which occurs when cells are stimulated e.g. by nitrogen. Example, profilin I (human): database code PRO1_HUMAN, 139 amino acids (14.91 kDa).

proflavin 3,6-diaminoacridine; an **acridine** dye, molecules of which are capable of intercalating between adjacent base pairs in duplex DNA. It is useful as an antibacterial agent, by virtue of its ability to inhibit the biosynthesis of both DNA and RNA, possibly through intercalation into preexisting DNA, and as a frameshift mutagen for bacteriophages.



progesterone *the common name for* pregn-4-ene-3,20-dione; the principal steroid hormone of the corpus luteum, from which it is secreted during the latter half of the estrous cycle, acting upon the endometrium to prepare it for embryo im-

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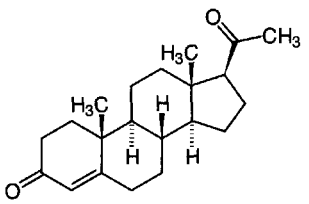
plantation. During pregnancy, secretion occurs also from the placenta, the rate of production increasing markedly as pregnancy proceeds, when it acts to maintain the uterus, inhibit further release of ova, and promote proliferation of acini within the mammary gland. Progesterone occurs also in the adrenal cortex and testis. It is synthesized from **pregnenolone** by 3β-hydroxy-Δ^5-steroid dehydrogenase, EC 1.1.1.145, and is an intermediate in the formation of androgens, estrogens, glucocorticoids, and mineralocorticoids. It also occurs in some plants, e.g. *Hollatrhena floribunda*.



progestin **1** *an alternative name for* **progestogen**. **2** natural **progesterone**, especially in unpurified form.

progestogen *or* **progestagen** *or* **progestin** any natural or synthetic compound with the hormonal activity of progesterone. In oral contraception regimes, a progestogen is normally combined with an estrogen. The effect is to inhibit ovulation. A preferred method is to use a gestagen, which acts by an effect on the endometrium; these have fewer side effects than progestogens.

proglucagon the putative prohormone of **glucagon** and **enteroglucagon**. In mammals it appears to be an 18 kDa single-chain polypeptide of some 170 residues that contains the entire 29-residue sequence of glucagon within its N-terminal moiety and in addition the sequences of two glucagon-like peptides, designated GLP-1 and GLP-2, of 37 and 35 residues respectively, within its C-terminal moiety. The 69-residue N-terminal portion of the molecule, containing the glucagon sequence, is identical with **glicentin**, and thus in mammals proglucagon appears to be the common biogenetic precursor both of pancreatic glucagon and of enteroglucagon and other nonpancreatic forms of glucagon. Angler-fish proglucagon is similar but smaller, and apparently exists in two forms: a 14 kDa form (lacking GLP-2 and a 13-residue connecting peptide) and a 12 kDa form (of unknown sequence).

program **1** a sequence of coded instructions for controlling a computer or other electrical or electromechanical device, especially for enabling a computer to manipulate data in a predetermined way; an equivalent of this in an electronic or magnetic storage medium. **2** to constrain to function or operate in a particular way, especially by providing with a program or other (set of) instructions. **3** to write (and test) a computer program for a specific application. —**programmable** *or sometimes (esp. US)* **programable** *adj.*

programmable messenger *a term proposed for* a cytosolic protein messenger molecule in a hypothesis advanced to explain the multiple actions on their target cells of hormones whose cellular receptors are linked to oligomeric GTP-regulatory proteins in cell membranes. According to this concept, the activation of GTP-regulatory proteins (by GTP and the respective hormones) causes release of their α subunits from the membranes as cytosolic proteins, which become the primary messengers of hormone action and which thereupon are transformed by various protein-modifying enzymes (e.g. kinases and proteases) to yield new structures with selective affinities for different effectors, each responsive to its specific activating system. A variety of responses of the target cells thus may be elicited: accordingly, these messengers are considered programmable.

programmed ribosomal frameshifting a mechanism whereby different proteins may result from a single mRNA molecule, due to the presence of alternative sites within the mRNA that are recognized for initiation and termination of translation.

progress curve a graph showing the change with time in the concentration or amount of an analyte as a chemical reaction proceeds.

prohormone a natural precursor of a hormone, especially for the proprotein of a (poly)peptide or protein hormone.

prohormone convertase an enzyme activity that cleaves prohormones at **dibasic cleavage sites** to form active polypeptides. As EC 3.4.23.17 its *recommended name* is proopiomelanocortin converting enzyme. However, no sequence has been reported. An example of a convertase enzyme is given in **kexin**. *See also* **neuroendocrine convertase**.

prohormone converting enzyme *see* **pro-opiomelanocortin converting enzyme**.

proinsulin *or (formerly)* **pro-insuline** the prohormone of **insulin**; it is a single-chain polypeptide of ≈9 kDa with three intrachain disulfide bridges, the number of amino-acid residues varying somewhat with species (78 in dog, 81 in cattle and sheep, 84 in cod and pig, 86 in horse, human, and rat). Proinsulin is synthesized in the pancreatic B cell, where it is normally present at about 5% of the concentration of insulin, and from where it is secreted in small amounts into the blood.

projection formula any two-dimensional diagrammatic representation of the (three-dimensional) structural formula of a molecule (or part thereof) as if seen by projection onto a plane surface from a particular viewpoint in space. Bonds with different spatial orientations relative to the observer may be depicted distinctively. The term includes **conformational formula**, **Fischer projection**, **Newman projection**, and **perspective formula**.

prokaryon *or* **procaryon** (*pl.* **prokarya** *or* **procarya**) a primitive nucleus; i.e. genomic DNA in a defined structure, but lacking a nuclear membrane or other nuclear inclusions. Such an arrangement is found in bacteria (including actinomycetes) and cyanobacteria. *See also* **nucleoid** (def. 2). —**prokaryous** *or* **procaryous** *adj.*; **prokaryosis** *or* **procaryosis** *n.*

prokaryosis the condition of possessing a prokaryon or prokarya.

prokaryote *or* **procaryote** any organism in which the genomic DNA is not enclosed by a nuclear membrane within the cells; i.e. any organism whose cells possess a **prokaryon**. The prokaryotes comprise the bacteria, cyanobacteria, and archaea and are classified in their own kingdom, variously named Monera or Procaryotae. *Compare* **eukaryote**. —**prokaryotic** *or* **procaryotic** *adj.*

prolactin *abbr.*: PRL; a hormone secreted by the anterior pituitary that stimulates lactation. Human prolactin (hPRL) is a 199-residue protein, 23 kDa in its monomeric form (**little prolactin**), although dimeric (**big prolactin**, 48–56 kDa) and polymeric (>100 kDa) forms circulate in blood. The prolactin gene belongs to a family of genes, along with those encoding placental lactogen and human growth hormone (*see* **somatotropin**). Secretion is episodic; it is inhibited by dopamine, which binds to lactotrope D_2 receptor (*see* **dopamine receptor**) to inhibit adenylate cyclase, and is probably stimulated by **thyrotropin-releasing hormone** and **vasoactive intestinal peptide**. Prolactin synthesis is positively regulated by estrogen acting at the level of the prolactin gene. Receptors for prolactin are located in breast, liver, ovary, testis, and prostate, but its main site of action is the mammary gland, which is stimulated to develop by estrogen, progesterone, prolactin, and placental mammotropic hormones. Lactation is stimulated by prolactin but is prevented during pregnancy by the inhibitory action of estrogen and progesterone, the levels of which fall after parturition, allowing prolactin to initiate lactation. Example (precursor) from *Gallus gallus*: database code PRL_CHICK, 229 amino acids (25.81 kDa). *See also* **prolactin receptor**, **proliferin**.

prolactin receptor a membrane protein of the cytokine receptor family. Example (type 2; precursor) from human; database

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code PLR2_HUMAN, 622 amino acids (69.43 kDa). The prolactin receptor is associated with a small protein **calcyclin**.

prolamin *or (formerly)* **prolamine** any of a group of simple proline-rich proteins, found especially in the seeds of cereal plants, that are insoluble in water, neutral salt solutions, and absolute ethanol, but soluble in dilute acid or alkali and in 70–80% aqueous ethanol. The group includes the **gliadins** of wheat and rye, **hordein** of barley, and **zein** of maize. *Compare* **glutelin**.

prolate **1** having a polar diameter longer than the equatorial diameter. **2** describing an **ellipsoid of rotation** generated by the rotation of an ellipse about its major axis. *Compare* **oblate**.

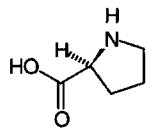
prolidase *another name for* **X-Pro dipeptidase**. *Distinguish from* **prolinase**.

proliferin *or* **mitogen-regulated protein** a prolactin-related protein, the mRNA of which appears in several murine cell lines during growth. One of several proteins of the somatotropin/prolactin family that provide a growth stimulus to target cells in maternal and fetal tissues during the development of the embryo. The mRNA occurs in placenta, which secretes proliferin as a glycoprotein distinct from placental lactogen. Examples: three proliferin precursors from mouse: database code PRO1_MOUSE, 224 amino acids (25.34 kDa); database code PRO2_MOUSE, 224 amino acids (25.28 kDa); and database code PRO3_MOUSE, 224 amino acids (25.31 kDa).

prolinase *the recommended name for* **Pro-X dipeptidase**. *Distinguish from* **prolidase**.

prolinate **1** proline anion; the anion, $(C_4H_7NH)–COO^-$, derived from **proline**. **2** any salt containing proline anion. **3** any ester of proline.

proline *the trivial name for* pyrrolidine-2-carboxylic acid, $(C_4H_7NH)–COOH$; a chiral cyclic *N*-alkylated α-amino acid. L-proline (*symbol*: P *or* Pro), (*S*)-pyrrolidine-2-carboxylic acid, is a coded amino acid found in peptide linkage in proteins; codon: CCA, CCC, CCG, or CCU; by virtue of its more constrained molecular structure relative to most other α-amino acids it cannot participate in α-helix formation. In mammals it is a nonessential dietary amino acid and is glucogenic. It is formed from **glutamate 5-semialdehyde** by reduction by NADPH. D-Proline (*symbol*: D-Pro *or* DPro), (*R*)-pyrrolidine-2-carboxylic acid, is not known to occur naturally. *See also* **hydroxyproline**.



L-proline

proline/arginine-rich protein *abbr.*: PARP; a 24 kDa proline- and arginine-rich protein from bovine cartilage, closely related to the N-terminal domain of collagen α1 (XI).

proline dehydrogenase EC 1.5.99.8; a flavoprotein enzyme that catalyses the reaction:

L-proline + acceptor + H_2O =
(*S*)-1-pyrroline-5-carboxylate + reduced acceptor.

The flavin is FAD. Example, from *Escherichia coli*, a bifunctional enzyme, having the activities of both proline dehydrogenase and **1-pyrroline-5-carboxylate dehydrogenase**: database code PUTA_ECOLI, 1320 amino acids (143.66 kDa).

proline dipeptidase *see* **X-Pro dipeptidase**.

proline hydroxylase *see* **procollagen-proline dioxygenase**.

prolinium proline cation; the cation, $(C_4H_7NH_2^+)–COOH$, derived from proline.

prolino the pyrrolidino group, $HOOC–(C_4H_7N)–$, derived from proline.

prolyl the acyl group, $(C_4H_7NH)–CO–$, derived from proline.

prolyl dipeptidase *see* **Pro-X dipeptidase**.

L-prolylglycine dipeptidase *see* **Pro-X dipeptidase**.

prolyl hydroxylase *see* **procollagen-proline dioxygenase**.

prolyl oligopeptidase EC 3.4.21.26; *other names*: prolyl endopeptidase; post-proline cleaving enzyme; post-proline endopeptidase. An enzyme that catalyses the hydrolysis of Pro-|-Xaa >> Ala-|-Xaa in oligopeptides. It is a cytoplasmic (in eukaryotes) serine endopeptidase, also found in some bacteria. Example from pig: database code PPCE_PIG, 710 amino acids (80.68 kDa).

prometaphase the stage in **mitosis** or **meiosis**, following **prophase**, during which the nuclear envelope is disrupted and breaks into membrane vesicles, and the spindle microtubules enter the nuclear region. **Kinetochores** mature on each **centromere** and attach to some of the spindle microtubules; these are then called **kinetochore microtubules** while those to which kinetochores do not attach are called **polar microtubules**; microtubules outside the spindle are called **astral microtubules**. Kinetochore microtubules begin the process of aligning chromosomes in one plane halfway between the poles.

promoter *symbol*: *P*; a DNA sequence located 5′ to a gene that indicates the site for the initiation of transcription. It may influence the amount of mRNA produced and the tissue specificity. Examples include the **TATA box**. The symbol may be subscripted to indicate particular promoters, e.g. P_{RM}, a promoter for the *cI* gene, RM standing for repressor maintenance.

promoter ligand an additional ligand that is included in the loading buffer in **affinity chromatography**, to promote specific binding to the immobilized ligand.

promutagen any substance that, when acted upon by the cell's metabolism, becomes a **mutagen**.

Pronase *a proprietary name for* a mixture of various exo- and endo-peptidases, obtained from *Streptomyces griseus*, that is able to hydrolyse virtually any protein almost completely to free amino acids. It is used for hydrolysis of many proteins, for digestion of mucins, in isolation of intact DNA or RNA from cells or viruses, and in dispersal of certain types of mammalian tissue cells, e.g. chondrocytes.

pronucleus (*pl.* **pronuclei**) the nucleus of either the ovum or the spermatozoon following fertilization. Thus, in the fertilized ovum, there are two pronuclei, one originating from the ovum, the other from the spermatozoon that brought about fertilization; they approach each other, but do not fuse until just before the first cleavage, when each pronucleus loses its membrane to release its contents. —**pronuclear** *adj.*

proof a standard by which the strength of distilled alcoholic solutions (or vinegars) is judged. In the UK it is the strength of a mixture of alcohol and water having a specific gravity of 0.91984, and containing 0.495 of its weight or 0.5727 of its volume of absolute alcohol. Degrees of proof express the percentage of proof spirit present; hence 70° proof spirit contains 0.7 × 57.27% alcohol. In the US, proof is a number that is twice the percentage (by volume) of alcohol present; hence 70° proof spirit contains 0.5 × 70% alcohol.

proofreading *(in genetics)* verification of the exact nature of a sequence of bases in DNA or amino-acid residues in a protein. Proofreading of DNA sequence occurs in transcription, during the action of DNA polymerase, when incorporation of an incorrect nucleotide causes mismatch in pairing with the complementary base on the template strand; this leads to immediate excision of the incorrect nucleotide, retreat of the enzyme to the previous position, and another attempt to insert the correct nucleotide. During translation, charging of the tRNA with its aminoacyl group is verified by its fit in the binding site; if incorrect, the aminoacyl-tRNA is hydrolysed to tRNA and amino acid and the whole process is repeated until successful. Examples of such proofreading during translation include rejection of threonine by valine–tRNA ligase, and of valine by isoleucine–tRNA ligase. *See also* **mismatch repair**.

Pro(3-OH) *symbol for* a residue of the α-amino acid (*trans*-)3-hydroxy-L-proline (alternative to 3Hyp).

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Pro(4-OH) *symbol for* a residue of the α-amino acid (*trans*-)4-hydroxy-L-proline (alternative to 4Hyp).

proopiomelanocortin *abbr.*: POMC; a 241-residue prohormone protein, *also called* **corticotropin–lipotropin precursor**, synthesized in the intermediate and anterior lobes of the pituitary as the primary gene product of the POMC gene; in humans this is located on chromosome 2. POMC is enzymically cleaved in the anterior pituitary by a **prohormone convertase**, PC1 to yield an N-terminal peptide (residues 1–80), **corticotropin** (residues 110–148) and β **lipotropin** (β-LPH, residues 148–241). The segment 83–107, which is thus released, is known as **joining peptide**. Prohormone convertase, PC2, then cleaves corticotropin to yield α-**melanocyte-stimulating hormone** (α-**MSH**; residues 110–122), and cleaves β-LPH to yield γ-LPH (residues 151–208) and β **endorphin** (residues 211–241). Example from human: database code COLI_HUMAN, 267 amino acids (29.39 kDa) residues 1–26 being the signal peptide. Derived hormones (cleavage points and some sizes differ from porcine above): corticotropin, 39 amino acids; **corticotropin-like intermediate lobe peptide**, 21 amino acids; β endorphin, 31 amino acids; lipotropins β-LPH (89 amino acids) and γ-LPH (56 amino acids); melanocyte-stimulating hormones α-MSH (13 amino acids), β-MSH (18 amino acids), and γ-MSH (11 amino acids); [Met]enkephalin (*see* **enkephalin**), 5 amino acids. In the intermediate lobe, POMC synthesis is regulated mainly by dopamine and serotonin; in the anterior lobe by glucocorticoids and corticotropin-releasing hormone. The prohormone convertases are related to **furin** and **kexin**.

proopiomelanocortin converting enzyme EC 3.4.23.17; *the recommended name for* **prohormone convertase**.

propargylamine *see* **monoamine oxidase inhibitors**.

propellant *or* **propellent** any substance that through pressure or combustion or other means causes propulsion, as, e.g., the use of compressed gases in spray cans.

propeptide that part of a peptide chain that follows the signal sequence, and which is cleaved off in formation of the mature protein.

properdin *see* **complement**.

prophage a form of the genome of a bacteriophage in which the nucleic acid is integrated into the genome of the phage's bacterial host, a state known as **lysogeny**. Activation to produce mature phage can occur, with accompanying lysis of the bacterium. For example, in **lambda phage**, transcription of the prophage is repressed by a gene, *c*I, that codes for a repressor protein that binds to the operator (*O*) genes to prevent use of the promoter (*P*) genes. The product of the *c*II gene, CII, is critical in determining the switch between lysogeny and lysis; if CII is not active (e.g. due to breakdown by host proteases) lysogenization is favoured, since CII competes with the repressor product of *c*I and prevents it binding to *O*.

prophage induction *see* **phage induction**.

prophage-mediated conversion *another name for* **bacteriophage conversion**.

prophage reactivation the phenomenon in which the survival of UV-irradiated **lambda phage** is higher in a host carrying a homologous heteroimmune prophage than in a host that is nonlysogenic or is lysogenic with a nonhomologous prophage.

prophase the initial stage of **mitosis** or **meiosis** in which the chromosomes are condensed, becoming apparent within the nucleus, but are not yet attached to a mitotic spindle. By early prophase, the single centrosome contains two centriole pairs; at late prophase, the centrosome divides and the two asters move apart. In meiosis, the chromosomes come together in homologous pairs, and undergo crossing-over. This occurs during the first of the two meiotic cell divisions, and is divided into several stages. In the first, zygotene, a complex structure develops between the two sister chromatids of each pair, which may play a part in **recombination**. They remain in the complex during a stage known as pachytene, then separate at the diplotene stage.

propheromone convertase Y a protease present in yeast with specificity towards paired basic residues (-Lys-Arg-, -Arg-Arg-, or -Arg-Lys-) and no activity towards single basic residues.

propionate the anion, $CH_3–CH_2–COO^-$, derived from propionic acid, in any salt; designation for the **propionyl** radical in naming an ester.

propionibacteria bacteria belonging to the genus *Propionibacterium*. They are characterized by their activity in fermenting glucose or lactic acid to propionic acid; acetic acid is also a major product. *See also* **propionic-acid fermentation**.

propionic acid propanoic acid; $CH_3–CH_2–COOH$; a carboxylic acid, important in the energy metabolism of ruminants, in which it is formed by rumen bacteria. It is the basis of a series of nonsteroidal anti-inflammatory agents, known as substituted propionic acids; *see* **ibuprofen**.

propionic-acid fermentation fermentation of glucose or lactate by *Propionibacterium* spp. (*see* **propionibacteria**) to either propionate or acetate; pyruvate is a common intermediate for both transformations, the pathway then branching to form either propionate or acetate. In propionate formation, pyruvate first reacts with methylmalonyl-CoA to form propionyl-CoA and oxaloacetate. The latter is converted by reactions of the tricarboxylic-acid cycle to succinate, which then reacts with the propionyl-CoA to form propionate and succinyl-CoA. The succinyl-CoA is converted to methylmalonyl-CoA, which is then available to react with a further molecule of pyruvate. Conversion of pyruvate to acetic acid involves oxidative decarboxylation to acetyl-CoA, reaction of this with orthophosphate to form acetyl phosphate, and reaction of the latter with ADP to form ATP and acetic acid. When lactate is the initial substrate, this is first converted to pyruvate by lactate dehydrogenase. This enzyme is a flavoprotein, that is oxidized by a cytochrome *b*.

propionyl *symbol*: Pp; *the trivial name for* propanoyl, $CH_3–CH_2–CO–$, the univalent acyl group derived from propionic (i.e. propanoic) acid.

propionyl-CoA carboxylase *abbr.*: PCCase; EC 6.4.1.3; an enzyme that catalyses a reaction between ATP, propanoyl-CoA, and HCO_3^- to form (*S*)-methylmalonyl-CoA, ADP, and orthophosphate; biotin is a coenzyme. It is an enzyme in the catabolic pathways of odd-chain fatty acids and isoleucine, occurring in the mitochondrial matrix. Defects cause propionic acidemia, which is inherited as a recessive trait. Example from human (precursor); six α chains (biotin binding): database code PCCA_HUMAN, 702 amino acids (77.01 kDa); and six β chains: database code PCCB_HUMAN, 155 amino acids (16.99 kDa).

proplastid the precursor of a **plastid**.

propolypeptide the inactive form in which some polypeptide hormones or other agonists are produced; it is then activated by removal of part of the sequence by a proteinase.

proportional counter any device for measuring radioactive disintegrations by means of a gas-filled ionization chamber, e.g. Geiger counter, operating in the **proportional region**.

proportional region a range of voltages applied to a gas-filled ionization chamber (e.g. Geiger counter) over which the gas amplification is greater than unity. In radioactive counters of this type, measurement depends on ionization of the gas in the ionization chamber by emitted radiation. Up to a certain applied voltage, ion production and thus the current through the chamber depends solely on collisions between emitted radiation and gas molecules; at higher voltages, the current is enhanced by additional collisions, so that sensitivity is increased, but the current remains proportional (hence the name proportional region) to the rate of emission of radiation. *Compare* **Geiger region**.

propositus *or (fem.)* **proposita** (*pl.* **propositi**) *or* **proband** the first individual to present as a patient, in a series of cases related (usually) to a heritable disorder, and from whom the line of descent is traced.

propranolol an important β-adrenoceptor antagonist; the (*S*)

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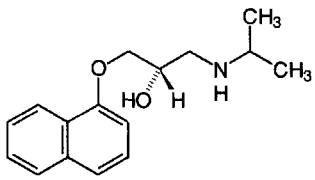
form is the active structure. It is used therapeutically as an antihypertensive, anti-anginal, and anti-arrhythmic. *One proprietary name*: Inderal (as hydrochloride).



(*S*)-form

propressophysin the polypeptide precursor of **vasopressin** and **neurophysin** (*see* **vasopressin–neurophysin 2–copeptin precursor**). A clinical name for the product of the gene associated with familial neurogenic diabetes insipidus.

proprotein an inactive form of a protein, having an additional sequence that is removed by a proteinase to yield the active protein; a classic example is **proinsulin**. A **zymogen** is a form of proprotein, sometimes referred to as a proenzyme.

propyl *symbol*: Pr; *n*-propyl; the alkyl group, $CH_3–CH_2–CH_2–$, derived from propane. *Compare* **isopropyl**.

***pro-R/pro-S* convention** stereochemical descriptors for paired, chemically-like ligands at a prochiral centre; they derive from an extension of the **sequence rule** used to assign *R,S* descriptors to a chiral centre. In the prochiral (but achiral) structure, *Caabc*, the chemically-like ligands are the two atoms (or groups of atoms), *a*. For the sake of example assume that the sequence rule gives the priority sequence, $a > b > c$. In the molecular model (or projection formula) arbitrarily label the *a* groups as a' and a'' and arbitrarily assign higher priority to one of them, e.g., $a' > a''$. The modified priority sequence, $a' > a'' > b > c$, is then considered with the model viewed from the side remote from *c*. If this gives a right-handed ordering for $a' \rightarrow a'' \rightarrow b$, thus leading to *R* chirality for the arbitrarily created chiral element, the promoted a' is designated the *pro-R* group; conversely, if the arbitrarily created chiral element reveals an *S* ordering, the promoted group is *pro-S*. Example: glycerol, $HOCH_2–CHOH–CH_2OH$, contains two chemically-like CH_2OH groups, and the normal priority sequence is OH > CH_2OH > H. In the **Fischer projection** formula with the central carbon atom having the OH group to the right and H to the left, arbitrarily assign the top $C'H_2OH$ group priority over that at the bottom, $C''H_2OH$, giving the modified sequence, OH > $C'H_2OH$ (top) > $C''H_2OH$ (bottom) > H. When the model is viewed from the side remote from the lowest priority atom (H) the ordering, OH → $C'H_2OH$ (top) → CH_2OH (bottom) is right-handed so that the arbitrarily created chiral element has *R* chirality; hence the top $C'H_2OH$ is the *pro-R* group. Subscript letters *R* and *S* can be used to indicate whether an atom or group of atoms is *pro-R* or *pro-S*. This is most commonly done for the two hydrogens of a methylene group, with H_R indicating the *pro-R* hydrogen and H_S the *pro-S* hydrogen. For a methylene group, replacement of ^1H_R by ^2H or ^3H gives a centre with *R* chirality; similar replacement of ^1H_S gives a centre with *S* chirality. *See also* **enantiotopic**.

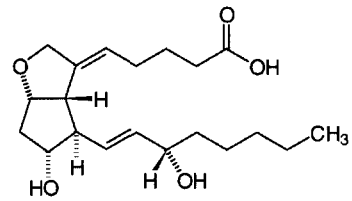
pros a designator of position of a nitrogen in the histidine imidazole ring, being that nitrogen nearest to the side chain; often abbreviated to π, as in N^{π}. *Compare* ***tele***.

PROSITE a database of all documented protein **motifs**.

prosolin *see* **stathmin**.

prosome *another name for* **proteasome**.

prostacyclin *or* **prostaglandin I** (*abbr.*: PGI) any of a group of prostanoids synthesized by **prostaglandin-I synthase** (EC 5.3.99.4) from prostaglandin H – which itself is the product of **prostaglandin-endoperoxide synthase** – as prostaglandin I_2, I_1, or I_3, depending on whether the substrate for the enzyme is arachidonate, dihomo-(6,9,12)-linolenate, or eicosa-5,8,11,14,17-pentaenoate respectively. PGI_2 is the major product *in vivo*; it is produced by endothelial cells of blood-vessel walls, has potent platelet anti-aggregatory properties resulting from stimulation of adenylate cyclase, and induces vasodilation. It has a normal half-life of 2 min, being degraded by hydrolysis to 6-oxo-prostaglandin $F_{1\alpha}$; this is then converted to the 6,15-dioxo-13,14-dihydro-$PGF_{1\alpha}$, and follows a similar degradative path to other prostaglandins. More stable but still active analogues have been synthesized, e.g. carbacyclin. (*S*)-15-hydroperoxyeicosatetraenoate inhibits prostaglandin-I synthase. *See also* **prostaglandin**.



prostaglandin I_2

prostacyclin synthase *see* **prostaglandin-I synthase**.

prostaglandin *abbr.*: PG; any of a group of biologically active metabolites of arachidonate (PG_2 series), dihomo-γ-linolenate (PG_1 series), or eicosa-5,8,11,14,17-pentaenoate (PG_3 series). They characteristically contain a cyclopentane ring due to formation of a bond between C-18 and C-12 of the fatty acid; hydroxy or oxo substitution at positions 9 and 11 is a major distinguishing feature between prostaglandin classes. They were originally discovered as a uterus-contracting activity in seminal plasma, and are now known to possess a protean array of highly potent biological activities that defy simplification. However, to give an indication of these roles, their pharmacological effects include: vasodilation (PGE_2 and **prostacyclin**) which is short-acting, and vasoconstriction ($PGF_{2\alpha}$ and **thromboxane** A_2); oxytocic activity ($PGF_{2\alpha}$ can be used to terminate pregnancy in the second trimester and PGE_2 induces labour at term); bronchodilation (PGE series) and constriction (PGF series). They are involved in inflammatory reactions, and the enzymes that are involved in their synthesis are targets for antiinflammatory agents such as aspirin and non-steroidal antiinflammatory drugs such as ibuprofen. They are also involved in the regulation of cell proliferation in normal and neoplastically transformed cells. Prostaglandins are formed from the precursors prostaglandin G_1, G_2, or G_3, the intermediate products of **prostaglandin-endoperoxide synthase**, depending on the substrate fatty acid; the same enzyme converts these to prostaglandins H, from which other enzymes form prostaglandins D, E, and F, and also **prostacyclins** (or prostaglandins I). These are, from the bioactive aspect, the end products of the system, but they have a half-life of minutes, being rapidly converted to metabolites with much weaker, or often inhibitory properties. The initial metabolites are the 15-oxo-13,14-dihydroprostaglandins, produced by the sequential actions of 15-hydroxyprostaglandin dehydrogenases (e.g. EC 1.1.1.196 and 1.1.1.197) and 15-oxoprostaglandin 13-reductase (EC 1.3.1.48); these are further degraded by beta oxidation and omega oxidation to urinary metabolites such as 7α-hydroxy-5,11-dioxotetranorprostane-1,16-dioate (from PGE_2) and 5,7-dihydroxy-11-oxotetranorprostane-1,16-dioate. The structures of prostanoic acid, with its carbon numbering, and of PGG_2, PGH_2, PGD_2, PGE_2 and $PGF_{2\alpha}$ are shown

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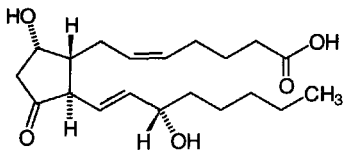
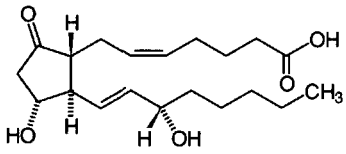
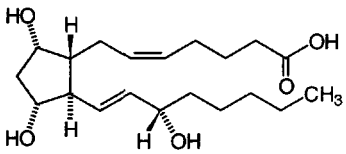


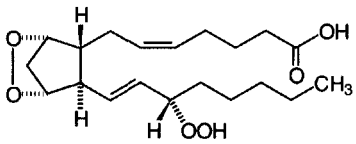
prostaglandin D_2



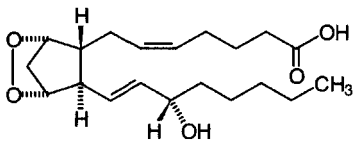
prostaglandin E_2



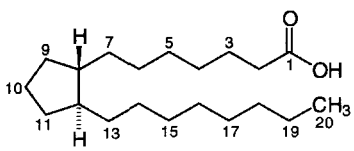
prostaglandin $F_{2\alpha}$



prostaglandin G_2



prostaglandin H_2



prostanoic acid

prostaglandin-D synthase *abbr.*: PGD synthase; EC 5.3.99.2; *other name*: prostaglandin-H_2 D-isomerase; an enzyme that catalyses the conversion of (5*Z*,13*E*)-(15*S*)-9α,11α-epidioxy-15-hydroxyprosta-5,13-dienoate to (5*Z*,13*E*)-(15*S*)-9α,15-dihydroxy-11-oxoprosta-5,13-dienoate (prostaglandin D). Glutathione is a cofactor in some cases. Example (precursor) from human, PGD_2 synthase (glutathione-independent PGD synthetase *or* β-trace protein): database code PGHD_HUMAN, 190 amino acids (21.00 kDa).

prostaglandin-endoperoxide synthase EC 1.14.99.1; *other names*: prostaglandin synthase; prostaglandin G/H synthase. An enzyme whose reaction embraces the activity formerly referred to as **cyclooxygenase**; it catalyses a reaction between dioxygen, arachidonate and two molecules of reduced glutathione (GSH) to form prostaglandin H_2, oxidized glutathione (GSSG), and H_2O. The enzyme acts as both a dioxygenase and as a peroxidase. It catalyses the formation of the precursor, prostaglandin G_2 (PGG_2), for the biosynthesis of all prostanoid compounds, by forming an endoperoxide bridge between C-9 and C-11, simultaneously bonding C-8 and C-12 to form the cyclopentane ring, and also forming the hydroperoxide at C-15. The latter is reduced by a reduced glutathione (GSH)-dependent peroxidase activity of the enzyme to a hydroxyl group to form prostaglandin H_2; these, and their further metabolites, prostaglandins D, E and F, are highly potent bioactive compounds with a great diversity of actions (*see* **prostaglandin**). The enzyme can also act on dihomo-(6,9,12)-linolenic acid, to form a series of prostaglandins (denoted by a subscript 1, e.g. PGE_1) lacking the C-5 double bond, and on eicosa-5,8,11,14,17-pentaenoic acid, to form the 3 series of prostaglandins (e.g. PGE_3), with the additional double bond at C-17. Two isoenzymes, COX-1, constitutively expressed, and COX-2, inducible in inflammation by cytokines, are highly homologous membrane proteins, but selective inhibition of COX-2 is possible due to its larger inhibitor-binding site. Aspirin acetylates an active-site serine residue in both, the IC_{50} being 10 to 100 times lower for COX-1 than for COX-2. Its inhibiton of COX-1 is the basis of its antithrombotic effects. Examples, both from human, COX-1 (precursor): database code PGH1_HUMAN, 599 amino acids (68.58 kDa); COX-2 (precursor): database code PGH2_HUMAN, 604 amino acids (68.98 kDa). *See also* **prostacyclin**, **thromboxane**.

prostaglandin-E_2 9-reductase EC 1.1.1.189; an enzyme that catalyses the reduction by NADPH of (5*Z*,13*E*)-(15*S*)-11α,15-dihydroxy-9-oxoprosta-5,13-dienoate (PGE_2) to (5*Z*,13*E*)-(15*S*)-9α,11α,15-trihydroxyprosta-5,13-dienoate ($PGF_{2\alpha}$) with formation of $NADP^+$. The monomeric cytoplasmic human enzyme catalyses reduction of many carbonyl compounds. In addition to the activity of prostaglandin-E_2 9-reductase (also termed prostaglandin 9-ketoreductase) described here two other activities are present. They are that of carbonyl reductase (NADPH) EC 1.1.1.184, and 15-hydroxyprostaglandin dehydrogenase ($NADP^+$), EC 1.1.1.197: database code DHCA_HUMAN, 276 amino acids (30.21 kDa).

prostaglandin-E synthase EC 5.3.99.3; *other names*: prostaglandin-H_2 E-isomerase; endoperoxide isomerase; an enzyme that catalyses the conversion of (5*Z*,13*E*)-(15*S*)-9α,11α-epidioxy-15-hydroxyprosta-5,13-dienoate to (5*Z*,13*E*)-(15*S*)-11α,15-dihydroxy-9-oxoprosta-5,13-dienoate (PGE_2). Glutathione is a cofactor.

prostaglandin-F synthase EC 1.1.1.188; *other name*: prostaglandin-D_2 11-reductase; an enzyme that catalyses the formation of (5*Z*,13*E*)-(15*S*)-9α,11α,15-trihydroxyprosta-5,13-dienoate and $NADP^+$ from (5*Z*,13*E*)-(15*S*)-9α,15-dihydroxy-11-oxoprosta-5,13-dienoate and NADPH. It is a monomeric protein of the prostaglandin biosynthetic pathway. Example of bovine enzyme (precursor): database code PGFS_BOVIN, 322 amino acids (36.55 kDa).

prostaglandin-I synthase EC 5.3.99.4; *other name*: prostacyclin synthase; an enzyme that catalyses the conversion of (5*Z*,13*E*)-(15*S*)-9α,11α-epidioxy-15-hydroxyprosta-5,13-dienoate to (5*Z*,13*E*)-(15*S*)-6,9α-epoxy-11α,15-dihydroxyprosta-5,13-dienoate (PGI_2, prostacyclin). This is a heme-thiolate protein. Example from human: database code JC2231, 500 amino acids (57.04 kDa).

prostanoate the anion of prostanoic acid, 2-octylcyclopent-

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aneheptanoic acid; the 8*S*,12*S* form is the parent compound for prostanoid nomenclature. For structure, *see* **prostaglandin**.

prostanoid any compound based on or derived from the **prostanoate** structure, including the **prostaglandins**, **prostacyclins**, and **thromboxanes**.

prostasin a serine protease with trypsin-like activity, found in human seminal fluid.

prostate–specific antigen *abbr.*: PSA; a proteinase which is virtually prostate specific. Levels may be elevated in prostate hypertrophy but the release into the serum from cancer is higher than from normal tissue. It is a much better marker than **acid phosphatase**, being elevated at an earlier stage of the tumour. PSA is a serine endopeptidase belonging to the family of glandular **kallikreins** with a His-Asp-Ser **charge-relay system**. Its physiological substrate is the predominant protein of the seminal vesicle coagulum. It can be isolated from prostate epithelial cells and seminal plasma. Example from human (precursor): database code PROS_HUMAN, 261 amino acids (28.74 kDa); residues 1–18 are a signal sequence, 19–24 a propeptide, and 25–261 PSA.

prostatic of, pertaining to, or related to the prostate gland.

prosthetic group a nonprotein group that is combined specifically with a protein, in stoichiometric proportion.

protachykinin β precursor a preproprotein from which certain polypeptide hormones are cleaved, not all by the same processing pathway. Example from human: database code TKNB_HUMAN, 129 amino acids (14.99 kDa). Derived peptides: **substance P**, residues 58–68; **neurokinin A**, residues 98–107; **neuropeptide K**, residues 72–107; residues 68 and 107 are C-amidated in the derived peptides. *See also* **tachykinin**.

protamine any of a group of small peptides, containing arginine, alanine, and serine, that are isolated from the sperm of fish (e.g. salmon, herring, sturgeon, trout, and mackerel), but present in the sperm of all animals. They have a histone-like function in the chromatin of sperm, compacting sperm DNA into a condensed complex. Example, sperm protamine P1 from *Alouatta seniculus* (howler monkey): database code HSP1_ALOSE, 51 amino acids (6.82 kDa).

protamine sulfate a sulfated derivative of a **protamine**. Protamine sulfates combine with, and inactivate, **heparin**, and are used to prevent bleeding in heparin overdose.

protease *a former name for* any enzyme that catalyses the hydrolysis of peptide bonds in a protein or polypeptide. The specific names **endopeptidase**, **aminopeptidase**, and **carboxypeptidase** are now recommended. *See also* **proteinase**.

protease inhibitor 4 *see* **kallistatin**.

protease nexin I *see* **nexin 1**.

proteasome *or* **proteosome** EC 3.4.99.46 *recommended name*: multicatalytic endopeptidase complex; *other names*: multicatalytic proteinase (complex); ingensin; macropain; prosome; lens neutral proteinase. Proteasomes are large multi-subunit protease complexes that selectively degrade intracellular proteins. Most of the proteins removed by these proteases are tagged for destruction by ubiquitination. Proteasomes play a role in controlling cellular processes, such as metabolism and the cell cycle, through signal-mediated proteolysis of key enzymes and regulatory proteins. They also operate in the stress response, by removing abnormal proteins, and in the immune response, by generating antigenic peptides. The proteolytic activity is due to a 26S protease, which is a 2 MDa complex. The ability of this 26S protease to degrade proteins generally depends on both the ubiquitination of the substrate and the presence of ATP. The core of the 26S protease is a 20S particle that carries the catalytic activity. It is this 20S particle that was first isolated, and was called 'multicatalytic proteinase' because it possessed trypsin-like, chymotrypsin-like and peptidyl-glutamyl activities, with the ability to cleave peptide bonds carboxy-terminal to basic, hydrophobic, and acidic residues. The 20S particle does not require ATP for activity. Following the determination of the crystal structure of this core from the Archaeon *Thermoplasma acidophilum*, the structure has been clarified. The proteasome itself is inactive and requires two specific subunits of a 19S particle to mediate recognition of ubiquitin–protein conjugates. The proteasome subunits are arranged in four heptameric rings which are stacked together to form a hollow cylinder with the protease activity on the inside. The active site nucleophile is threonine. The size of the channel in the cylinder is such that the protein substrate first must be unfolded and the disulfide bonds reduced. In *Thermoplasma*, the two outer rings of the 20S proteasome are composed of seven α subunits, and each inner ring contains seven β subunits, an organization that is likely also to apply in eukaryotic 20S proteasomes. The enzyme catalyses the cleavage at Xaa-|- bonds in which Xaa carries a hydrophobic, basic, or acidic side chain. Components (all examples are human): c2 (*other names*: macropain subunit c2; proteasome ν chain; multicatalytic endopeptidase complex subunit c2; 30 kDa proteasomal protein): database code PRC2_HUMAN, 263 amino acids (29.52 kDa); c3 (EC 3.4.99.46; *other names*: macropain subunit c3; multicatalytic endopeptidase complex subunit c3): database code PRC3_ HUMAN, 233 amino acids (25.74 kDa); c5 (*other names*: macropain subunit c5; proteasome γ chain): database code PRC5_HUMAN, 241 amino acids (26.46 kDa); proteasome chain 7 (*other names*: macropain chain 7; multicatalytic endopeptidase complex chain 7; ring 12 protein): database code PRC7_HUMAN, 219 amino acids (23.24 kDa); proteasome component c8 (*other names*: macropain subunit c8; multicatalytic endopeptidase complex subunit c8): database code PRC8_HUMAN, 254 amino acids (28.27 kDa); proteasome component c9 (*other names*: macropain subunit c9; multicatalytic endopeptidase complex subunit c9): database code PRC9_HUMAN, 261 amino acids (29.45 kDa); proteasome β chain (*other names*: macropain β chain; multicatalytic endopeptidase complex β chain (fragment)): database code PRCB_HUMAN, 28 amino acids (2.79 kDa); component c13 (*other names*: macropain subunit c13; multicatalytic endopeptidase complex subunit c13): database code PRCC_HUMAN, 208 amino acids (23.03 kDa); δ chain (*other names*: macropain δ chain; multicatalytic endopeptidase complex δ chain): database code PRCD_HUMAN, 205 amino acids (21.68 kDa); ε chain (*other names*: macropain ε chain; multicatalytic endopeptidase complexε chain; proteasome chain 6 (fragment)): database code PRCE_HUMAN, 26 amino acids (2.32 kDa); component mecl-1 (*other names*: macropain subunit mecl-1; multicatalytic endopeptidase complex subunit mecl-1): database code PRCF_HUMAN, 273 amino acids (28.90 kDa); τ chain (*other names*: macropain τ chain; multicatalytic endopeptidase complex τ chain; 27 kDa proteasomal protein (also in rat)): database code PRCI_HUMAN, 246 amino acids (27.37 kDa); ζ chain (*other names*: macropain ζ chain; multicatalytic endopeptidase complex ζ chain): database code PRCZ_HUMAN, 241 amino acids (26.44 kDa).

protectin *see* **CD59**.

protecting group *or* **protective group** *or* **blocking group** any chemical group added to a reactive centre of a molecule to prevent it from reacting during chemical treatments in which it is not intended to participate. Such groups are commonly used during chemical synthesis of macromolecules or shorter polymers of amino acids or nucleotides. Reagents contributing protecting groups should react readily under mild conditions, with high specificity, and lead to addition of a group that can be removed highly specifically under mild conditions. For protein or amino-acid protecting groups *see* **aminoethyl**, **Boc**, **citraconylation**, **DABITC**, **dabsyl**, **dansyl**, **Fmoc**, **maleylation**, **pipsyl**, **silylation**, **succinylation**, **tosyl**, **triphenylmethyl group**.

protegrin *abbr.*: PG; any of a group of leukocyte antimicrobial peptides, denoted PG-1 to PG-5, that are active against *Escherichia coli*, *Listeria monocytogenes*, and *Candida albicans in vitro*. Like **tachyplesins** they contain two intramolecular cystine disulfide bonds and show homology to **defensins**. Example, protegrin 1 (precursor) from *Sus scrofa*: database code

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PG1_PIG, 149 amino acids (16.67 kDa); protegrin 1 is residues 131–148.

protein any of a large group of organic compounds found as major macromolecular constituents of living organisms. All enzymes are proteins, although catalytic activity is shown by some nucleic-acid molecules (*see* **ribozyme**). A protein is a linear polymer of **amino acids** linked by peptide bonds in a specific sequence. In the biosynthesis of the polypeptide chain, any of 20 different amino acids may be incorporated, according to the genetic instructions of the cell (*see* **protein and peptide biosynthesis**). The amino-acid residues may be modified subsequently so that the chains may contain a much wider variety of residues, amounting to nearly 200. The modifications may involve the covalent attachment of various groups such as carbohydrates and phosphate; these are the simple proteins. Other substances may be more loosely associated with the polypeptide chains, such as heme or lipid, giving rise to the **conjugated proteins**. Four hierarchies of structure may be detected in the polypeptide chains: **primary structure** is the order of the specific amino-acid residues; **secondary structure** is the way the amino-acid residues interact within a chain to form structures such as the alpha helix and the beta strand; **tertiary structure** signifies the way in which an entire single polypeptide chain (or chains linked by disulfide bonds) folds to form a three-dimensional structure; and **quaternary structure** is the interaction between intact chains to form multi-subunit proteins. The various ways in which the polypeptide chains fold have been elucidated, in particular with regard to the presence of **alpha helices** and **beta-pleated sheets**. Four types of proteins may be classified: all-alpha; all-beta; alpha/beta; and alpha + beta. Some important protein types are listed separately in this dictionary and many others are listed individually: contractile proteins (**actin**, **myosin**, **tropomyosin**, **tubulin**), **heat-shock proteins**, **hemoproteins** (**cytochromes**, **hemoglobin**, **myoglobin**), **lipoproteins**, **membrane proteins** (**ATPases**, **ion channels**, **rhodopsin**), nonheme proteins (**blood coagulation** factors, **serum albumin**, **serum globulin**), nuclear proteins (**histones**), **plasma proteins**, and structural proteins (**collagen**, **crystallin**, **keratin**). Nutritional aspects of protein metabolism include the fact that higher animals cannot synthesize certain of the amino acids required for protein synthesis; such amino acids are referred to as **essential amino acids**. Plants and most microorganisms can synthesize all of the amino acids required for protein synthesis and many others. The nutritional value of different proteins depends on their composition. Some proteins are of poor nutritional value due to lack of essential amino acids, e.g. gliadin, which lacks lysine, and zein, which lacks lysine and tryptophan. —**proteinaceous** *adj.*

14-3-3 protein any of a highly conserved family of proteins, widespread in higher eukaryotes, that seem to act as regulators in signal transduction or phosphorylation. The name derives from the migration position on DEAE–cellulose columns, and on starch-gel electrophoresis, of certain brain proteins that were the first members of the family to be studied. Members of this family have been implicated in regulation of **protein kinase C**, transcriptional regulation in plants, exocytosis, cell-cycle regulation, and interaction with **Raf** in the **MAP kinase** cascade. For example, 14-3-3 protein β (*other name*: protein kinase C inhibitor protein-1) from sheep activates tyrosine and tryptophan hydroxylases in the presence of Ca^{2+}/calmodulin-dependent protein kinase II. The bovine equivalent has an identical sequence: it is a homodimer: database code 143B_BOVIN, 244 amino acids (27.82 kDa).

protein A a bacterial cell-wall protein, found in many strains of *Staphylococcus aureus*, that can bind, without masking the antigen-binding site, to the Fc region of IgG. It binds weakly to human IgA, IgE, and IgM but fails to bind to human IgG_3 and IgD; it does not bind to cell Fc receptors. The purified protein or a preparation of cells of *S. aureus* that carry protein A is widely used as an immunochemical reagent, often in an immobilized form on affinity columns, for isolation and purification of immunoglobulins and, by forming ternary complexes, of antigens and immune complexes. It is also used as a binding reagent in enzyme-linked immunoassay, in histochemistry, and in blotting techniques.

protein and peptide biosynthesis the biochemical synthesis of proteins. Biochemists became actively concerned with the elucidation of the mechanism of protein synthesis from about 1950. The classical pathway was expected to involve the utilization of enzymes to synthesize peptide intermediates, which would sequentially be linked together, but it soon became apparent that the number of enzymes involved would be horrendous and, moreover, there was no evidence that such peptide intermediates existed in living cells. Although there was a suggestion that peptide bonds were synthesized by transpeptidation using **proteolytic enzymes**, on theoretical grounds there was increasing support for the concept that the amino acids would first be aligned on a template and then be sequentially linked by peptide bonds. Following the elucidation of one structure for DNA in 1953 it was confidently predicted that the template would be nucleic acid. Shortly after, in 1955, P. C. Zamecnik and his group in Boston demonstrated the synthesis of a polypeptide by the isolated **microsome** fraction from rat liver. This involved the presence of particles (**ribosomes**), a soluble extract of the cell, and ATP and GTP.

As will be described, the synthesis of most peptides in living cells depends on the presence of ribosomes. This includes the small peptide hormones, such as **oxytocin** and **vasopressin**, which are synthesized as **polyproteins**. Other peptides are not synthesized by means of ribosomes. Thus **glutathione** is synthesized by soluble enzymes in two steps. Many biologically active peptides, especially cyclic structures, are products of microorganisms. These include such antibiotic peptides as **gramicidin S**, the **tyrocidines**, and the **polymyxins**. The systems responsible for their synthesis consist of interacting multienzymes in which activated aminoacyl groups are transferred onto –SH groups to form intermediate thioesters. The multienzymes are unusual in size, ranging from 120 to 1700 kDa. The respective genes consist of repeating modules, each encoding the incorporation of one amino-acid residue. The genes are arranged in clusters associated with genes encoding auxiliary proteins for the synthesis of precursors, modifying enzymes, exporting proteins, and regulatory systems. In addition to the amino acids and ATP, *S*-adenosylmethionine is required as methyl group donor if *N*-methylated bonds are involved. Due to their complexity (cyclosporin synthase for example, integrates 40 reactions on one polypeptide chain), the multienzyme systems have low turnover numbers. It has been possible to set up cell-free systems for the production of various peptides and their analogues.

With respect to the synthesis involving ribosomes it was shown that the first step was the activation of the amino acids to form amino-acid **adenylates**. The amino acids were then transferred to an RNA present in the soluble extract of the cell, and so named soluble RNA but later termed **transfer RNA** (tRNA) to which the amino acids became attached by an ester linkage. The template was then found to be **messenger RNA** (mRNA), which associates with the ribosomes themselves. Although the ribosomes themselves contain much RNA it came as a surprise that this did not serve as a template. The **translation** of the triplet codons in mRNA to provide a polypeptide involves three steps: chain initiation, chain elongation (*see* **elongation factor**), and chain termination (*see* **release factor**). Chain initiation normally starts with the codon for methionine, **AUG**. For this purpose a unique initiator tRNA is involved. Many protein factors play a part in the three processes and five molecules of ATP and GTP participate. The ribosomes participate in a cycle during which they subdivide into their two subunits only to reassemble. Hence the synthesis of a peptide bond is a surprisingly expensive process in terms of cell physiology. The targeting of the newly synthesized proteins to their final destination is termed **protein kin-**

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esis. The mechanism of ribosomal protein synthesis is very similar in all types of cell but there are subtle differences between prokaryotes and eukaryotes, which account for the differential action of antibiotics such as chloramphenicol and cycloheximide. Apart from differences in the number and properties of the soluble factors the main difference involves chain initiation: in prokaryotes this is by way of formylmethionine while in eukaryotes, apart from mitochondria, this involves methionine.

proteinase name introduced in 1928 to distinguish a sub-class of **proteases** that catalyse the hydrolysis of peptide bonds more readily in an intact protein than in small peptides. It is still widely used. **Endopeptidase** is now recommended.

proteinase K EC 3.4.21.64; *recommended name*: endopeptidase K; *other name*: *Tritirachium* alkaline proteinase. A serine proteinase enzyme that catalyses the hydrolysis of keratin, and of other proteins with subtilisin-like specificity. Example from the fungus *Tritirachium album*: database code NRL_2PRK, 279 amino acids (28.88 kDa); 3-D structure of this, and with inhibitor bound, is known.

proteinase V8 *see* **glutamyl endopeptidase**.

protein B a cell-surface protein of group B *Streptococcus* species that binds specifically to the Fc region of human IgA, without affecting its antigen-binding capacity, but not to other immunoglobulins or serum proteins. It is used in enzyme-linked immunoassay and blotting techniques.

protein biosynthesis *see* **protein and peptide biosynthesis**.

protein-bound iodine *abbr.*: PBI; that fraction of iodinated molecules bound to protein in serum. It is due largely to thyroxine (T_4), 99.97% of which in human serum is present bound to the binding proteins T_4-binding globulin, T_4-binding prealbumin and albumin, but also to T_3, 99.7% of which is bound to the same proteins. Determination of PBI (now replaced by immunoassay) was used for estimation of blood thyroid hormones as a basis for assessment of thyroid function.

protein C a **vitamin K**-dependent glycoprotein that is the **zymogen** of a serine endopeptidase in normal blood plasma; M_r 62 000 (human), 54 300 (bovine). It is formed from a precursor, autoprothrombin IIA, which is cleaved into a light chain and a heavy chain held together by a disulfide bond to form protein C. Thrombin cleaves a tetradecapeptide from the amino end of the heavy chain; this reaction, which occurs at the surface of endothelial cells, is strongly promoted by thrombomodulin; protein C then becomes the enzyme protein C (activated), EC 3.4.21.69. This activated form specifically hydrolyses factors Va and VIIIa to inactive forms (in a reaction requiring phospholipid, calcium, and **protein S**), thereby acting as a potent anticoagulation factor; it contains 10–12 γ-carboxyglutamyl residues in the N-terminal 40 residues. Example (precursor) from human: database code PRTC_HUMAN, 461 amino acids (52.01 kDa). A congenital deficiency of protein C (usually autosomal dominant) is often not compatible with survival, or leads to hemorrhagic disease of the newborn. Protein C is so named because it eluated from columns as the third of four peaks labelled A, B, C, and D.

protein C23 *see* **nucleolin**.

protein C-binding protein *see* **apolipoprotein H**.

protein disulfide-isomerase EC 5.3.4.1; *other name*: disulfide rearrangase; an enzyme that enhances the rate of interchange in the groups attached to two or more intrachain or interchain disulfide bonds in a protein. It was originally described by Anfinsen in 1966 concerning the reversible denaturation of ribonuclease and then called 'rearrangase'. It has since been shown to be a **luminal protein** of the endoplasmic reticulum. It is a homodimer; two of its domains are homologous to **thioredoxin** of *Escherichia coli*. It is also the triacylglycerol transfer protein (MTP) that facilitates the incorporation of lipids into newly synthesized core **lipoproteins** within the endoplasmic reticulum. It serves as the β subunit of **procollagen-proline dioxygenase**. Examples: probable protein disulfide-isomerase er-60 precursor from human (*other names*: erp60; 58 kDa microsomal protein): database code ER60_HUMAN, 505 amino acids (56.64 kDa); precursor (human) of this and also prolyl 4-hydroxylase β subunit (EC 1.14.11.2) and cellular thyroid hormone binding protein (p55): database code PDI_HUMAN, 508 amino acids (57.04 kDa).

protein engineering the process whereby a protein of any desired primary structure can (in principle) be created by the use of recombinant DNA technology. The ability to express DNA in a bacterium such as *Escherichia coli* creates the potential to synthesize a protein with the desired primary structure. Bacteria cannot effect post-translational modifications so if these also are required a eukaryotic host cell such as yeast must be employed. In principle there are no problems with the proteins of bacterial cells but **introns** present in the genome of eukaryotic cells present a potential problem. This can be overcome by preparing complementary DNA, **cDNA**, which is synthesized by the use of the **mRNA** as template and the enzyme **reverse transcriptase**. There are several ways whereby the DNA for the required protein may be prepared by modification of the base sequence of the natural DNA. DNA may be used that contains inserts of synthetic oligonucleotides, or stretches replaced by these. Oligonucleotide-directed mutagenesis may be used to modify a single base to produce a protein with a single amino-acid replacement. This is done by preparing an oligonucleotide primer with the modified sequence which will base pair with the natural DNA around the site to be altered; a single base substitution still permits satisfactory pairing. The primer is elongated by DNA polymerase and the double-stranded circle closed by **DNA ligase**. A specific deletion can be obtained by cleaving a plasmid at two sites with a restriction enzyme and religating to form a smaller circle. A smaller deletion can be obtained by cutting a plasmid at a single site. The ends of the linear DNA are then digested with an exonuclease that removes nucleotides from both strands and the shortened piece of DNA is religated.

protein folding disease any disease that results from the abnormal folding of a protein. **Prion** diseases are examples of such diseases that can be inherited or acquired; **Alzheimer's disease** is a different type of disease, caused by alternative folding of proteins derived from the amyloid precursor.

protein G a bacterial cell-wall protein isolated from group G streptococci. Its properties and uses are similar to those of **protein A**, but it does not bind to IgM, IgD, or IgA; it does bind to all subclasses of human IgG, and animal immunoglobulins with which protein A does not react well.

protein gene product any one of the proteins or protein subunits synthesized biochemically on the basis of information encoded in a genome, whether generated at **translation** or by **post-translational modification**; the pattern of protein gene products formed or capable of being formed by an organism is unique to any one genotype. Individual proteins are often referred to using the symbol p followed by the relative molecular mass, e.g. p53. The protein may be further identified by adding an indication of its origin as a superscript, e.g. $p21^{ras}$. A protein gene product may also be referred to by the name of the gene that encodes it, but normal font is used instead of italics, with a capital initial followed by lower case characters, e.g. Src protein encoded by *SRC* gene.

protein-glutamate methylesterase a chemotaxis protein encoded by *cheB* (*see* **che**).

protein–glutamine γ-glutamyltransferase EC 2.3.2.13; *systematic name*: protein-glutamine:amine γ-glutamyltransferase; *other names*: transglutaminase, factor XIIIa; the enzyme activity of **blood coagulation** factor XIIIa. It forms inter- and intramolecular links between a γ-carboxyl group of a glutamine residue of a protein and the ε-amino group of a lysine residue, releasing ammonium ion. Its natural substrate is the **fibrin** monomer, and its function is to link these into polymers. The protein is a heterotetramer of two each of the A and B chain,

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the A chain bearing the catalytic activity. Examples from human, A chain: database code F13A_HUMAN, 731 amino acids (83.14 kDa); residues 1–37 are a propeptide that is cleaved from the A chain by thrombin in the conversion of factor XIII to XIIIa; B chain (precursor): database code F13B_HUMAN, 661 amino acids (75.49 kDa); residues 1–20 are the signal peptide; the molecule contains ten **Sushi domains**.

protein intron *see* **intein**; **splicing** (def. 3).

protein kinase any of a number of enzymes that phosphorylate one or more hydroxyl or phenolic groups in proteins, ATP being the phosphoryl-group donor. Two classes are recognized: those that phosphorylate seryl or threonyl hydroxyls, and those that phosphorylate tyrosyl phenolic groups. The first class contains enzymes that were classically identified as regulating pathways of intermediary metabolism (e.g. glycogen **phosphorylase kinase**); subsequently, protein kinase A (**cyclic-AMP-dependent protein kinase**) and **protein kinase C** were recognized in this class. Enzyme activity of the second class is found in some cytokine receptors such as **platelet-derived growth factor receptor** and **epidermal growth factor receptor** and in oncogene products such as that of *SRC*. Over 110 unique gene products are known to make up the protein kinase superfamily; important motifs include GXGXXG...AHK and APE...DXWSXG, which are common to both serine/threonine- and tyrosine-specific activities. The tyrosine-specific kinase activity associated with the cytoplasmic domains of certain cytokine receptors forms part of an important signal-transduction mechanism implicated in cell growth (*see* **tyrosine kinase**).

protein kinase A *an alternative name for* **cyclic-AMP-dependent protein kinase**.

protein kinase C *abbr.*: PKC; any of a family of **protein kinase** enzymes identified following discovery of a protein kinase requiring anionic phospholipid for activity, and regulated by diacylglycerol and Ca^{2+}. They phosphorylate hydroxyl groups in substrate serine and threonine residues. Several isoforms have now been characterized: α, β_1, β_2, γ, δ, ε, ζ, θ, η, ι, and μ. Four conserved regions are recognized, C_1, C_2, C_3, and C_4; C_3 and C_4 comprise the C-terminal half of the molecule and bear the active site, including the ATP-binding sequence GXGXXG...K. PKC-ε is Ca^{2+}-independent, and δ, ε, and ζ lack the homologous C_2 region. Activation of PKC occurs when plasma membrane receptors coupled to phospholipase C are themselves activated, releasing diacylglycerol. Phorbol ester tumour promoters can substitute for diacylglycerol in enzyme activation, which may indicate their mechanism of action, and much evidence points to PKC activation being involved in cell-growth stimulation. Inhibitors of PKC attract considerable interest, and include **bisindolylmaleimide**, 1-O-hexadecyl-2-O-methylglycerol, **melittin**, **phloretin**, **polymyxin** B, and **staurosporine**. Examples: α from *Bos taurus*: database code KPCA_BOVIN, 672 amino acids (76.84 kDa); β_2 from *Oryctolagus cuniculus*: database code KPC2_RABIT, 673 amino acids (76.97 kDa); δ from *Mus musculus*: database code KPCD_MOUSE, 674 amino acids (77.59 kDa).

protein kinesis the directed movement of proteins from their site of synthesis to specific targets within cells and the modulation by proteins of interactions among intracellular organelles. It is a factor in generating subcellular compartments and determining the way in which reactions are compartmentalized to control metabolic processes. It embraces the mechanisms for ensuring that proteins reach their site of action and that the amounts and locations of particular proteins are controlled during development, during the cell-division cycle, in combating pathological states of the cell, and during apoptosis.

protein mapping the resolution of a mixture of proteins into a two-dimensional pattern (i.e. map) by successive use of two differing separative procedures, as in isoelectric focusing followed by gradient gel electrophoresis, the pattern being rendered visible by an appropriate detection method.

protein phosphatase any enzyme that hydrolyses phosphate groups from proteins. Together with protein kinases, these enzymes control the state of phosphorylation of cell proteins and thereby provide an important mechanism for regulating cellular activity. Protein phosphatases are classified into several groups. **Class I enzymes** are mainly specific for seryl- or threonyl-phosphate. Within this class, phosphatase 1 is ATP,Mg^{2+}-dependent (AMD phosphatase); it consists of a catalytic subunit of 38 kDa and a modulator subunit of 23 kDa, which is subject to phosphorylation, thus activating the phosphatase. Phosphatase 2A is polycation-stimulated (PCS), being directly stimulated by protamine, polylysine, or histone H1; it constitutes a subclass of several enzymes activated by different histones and polylysine. These have a very high affinity for the tumour promoter **okadaic acid**. Phosphatase 2B (or **calcineurin**) is a heterodimer; one of the subunits, of 61 kDa, contains the catalytic site, a high-affinity calmodulin-binding site, and a binding site for the other subunit, a 19 kDa, Ca^{2+}-binding protein. Phosphatase 2C is a Mg^{2+}-dependent monomeric 43 kDa protein; it has been purified as myosin light chain phosphatase, but is active against the phosphorylated forms of glycogen synthase, 6-phosphofructo-1-kinase, pyruvate kinase, fructose 1,6-bisphosphatase, and 6-phosphofructo-2-kinase. **Class II enzymes** hydrolyse tyrosylphosphates, and are generally designated 'phosphatase 3'. They are subdivided into those that are cytoplasmic, and others that are membrane-bound and may have receptor properties. Example of phosphatase 2A from human: database code P2AA_HUMAN, catalytic subunit 309 amino acids (35.55 kDa); same in rabbit. This enzyme can modulate the activities of phosphorylase kinase *b*, casein kinase 2, mitogen-stimulated S6 kinase, and MAP-2 kinase. It is a cytoplasmic enzyme that exists in several oligomeric forms, all of which contain a catalytic (C) subunit (36–38 kDa) associated with one or both of two putatively regulatory subunits, the A subunit (61–65 kDa) and the B subunit (51–55 kDa). Example of protein tyrosine phosphatase, leukocyte antigen-related PTPase precursor from human: database code LAR_HUMAN, 1897 amino acids (211.60 kDa).

protein-N^{π}-phosphohistidine–sugar phosphotransferase EC 2.7.1.69; *systematic name*: protein-N^{π}-phosphohistidine:sugar N^{π}-phosphotransferase; *other name* enzyme II; any of a group of related membrane-bound bacterial enzymes, part of the **phospho*enol*pyruvate-dependent sugar phosphotransferase system** for the transport of hexoses across the cell membrane. It involves phosphorylation of a protein substrate (9.5 kDa), a phosphocarrier known as HPr. Individual enzymes are specific for a range of sugars. They catalyse the reaction:

protein N^{π}-phosphohistidine (HPr) + sugar = protein histidine + sugar phosphate;

example from *Escherichia coli*: database code PT2G_ECOLI, 477 amino acids (50.62 kDa).

protein S a single-chain glycoprotein occurring in blood, M_r 69 000. It is a vitamin K-dependent protein (not a proteinase) that promotes the binding of **protein C** to platelets, and functions as a cofactor for the anticoagulant activity of activated protein C. It is named after Seattle, where it was discovered.

protein splicing *see* **splicing**.

protein synthesis 1 *(in cell biology) see* **protein and peptide biosynthesis**. 2 *(in chemistry) see* **peptide synthesis** (def. 2).

protein thiotemplate mechanism *see* **thiotemplate mechanism**.

proteinuria the presence of protein in urine. Normal excretion of protein in human urine is less than 0.1 mg every 24 h, about half of which is **Tamm–Horsfall glycoprotein**, and about 20% is albumin. Protein may appear in urine due to extrarenal factors such as fever, strenuous exercise, or burns; direct involvement of the kidney occurs in the nephrotic syndrome, which may arise from several causes, such as diabetic nephropathy, cancer of the kidney, or various forms of glomerulonephritis of unknown etiology.

protein Z a major protein of barley endosperm albumin. It is

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structurally similar to a **serpin**, but its main role is as a storage protein, being especially rich in lysine. Database code PRTZ_HORVU, 399 amino acids (22 lysine), 43.23 kDa.

proteoclastic *an obsolete term for* **proteolytic**.

proteoglycan any **glycoprotein** in which the carbohydrate units are **glycosaminoglycans**.

proteolipid *a term variously applied to describe* certain hydrophobic membrane proteins, or any other protein, that has a lipid moiety covalently bound to one or more of its constituent amino acids. Many such proteins are soluble in chloroform–methanol, a property that was significant in their first identification.

proteoliposome a **liposome** into which a specific protein, or group of proteins, has been incorporated.

proteolysis degradation of a protein, usually by hydrolysis at one or more of its peptide bonds. —**proteolytic** *adj.*

proteolytic enzyme *see* **peptidase**.

proteome the complete expression profile of the proteins of an organism. *See also* **proteomics**.

proteomics the study of the **proteome** by the analysis of protein structure and composition.

proteosome *a variant spelling of* **proteasome**.

prothrombin *an alternative name for* factor II; *see* **blood coagulation**.

protide **1** *symbol*: $^{1}H^{-}$; a **hydride** (def. 1) ion derived from an atom of **protium**. **2** any **hydride** (def. 2) formed from protium. **3** *or* **protid** *a generic name embracing* protein, peptide, or amino acid, suggested by analogy with glucide and lipid(e). Its use in English is largely restricted to translations or abstracts from French. —**protidic** *adj.*

protio- *comb. form* indicating that one or more atoms of hydrogen in a hydrogen-containing chemical compound consists exclusively of **protium**.

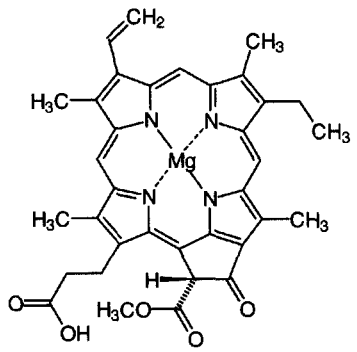
Protista a taxonomic grouping of eukaryotic organisms that are unicellular, coenocytic, or multicellular but that are not classified as fungi, animals, or embryophytes.

protium *symbol*: ^{1}H; hydrogen-1, the nuclide of hydrogen, $^{1}_{1}H$, of relative atomic mass 1.008. It is a stable isotope, having a relative abundance in natural hydrogen of 99.98 atom percent. The name is used especially when distinction from **deuterium** or **tritium** is required.

protoalkaloid an alkaloid that does not contain a heterocyclic ring, e.g. **damascenine** in *Nigella* spp.

protobiont one of the postulated first precursors of cells, supposed to have arisen when a boundary or membrane formed around one or more macromolecules possessing catalytic properties. *Compare* **coacervate droplet**.

protochlorophyllide Mg^{2+}-vinylpheoporphyrin A_5 methyl ether; an intermediate in the synthesis of chlorophyll, it is formed from Mg^{2+}-protoprophyrin, and converted to **chlorophyllide** by NADPH:protochlorophyllide oxidoreductase (EC 1.3.1.33). Protochlorophyllides may be suffixed with the letter of the related chlorophyll, e.g. protochlorophyllide *a*.



protochlorophyllide *a*

protochlorophyllide holochrome a pigment protein complex that carries out a light-catalysed reduction of **protochlorophyllide** to **chlorophyllide** with an external hydrogen donor, which is probably strongly bound NADPH. The enzyme involved in regenerating NADPH is **NADPH-protochlorophyllide oxidoreductase**; it is a single polypeptide, M_r 36 000, and is only one component of the complex protein entity of the holochrome.

protocollagen **collagen** chains in which proline and lysine residues have not been hydroxylated. Protocollagens may be produced by experimental inhibition of the relevant hydroxylases either by use of a chelating agent or by imposed anaerobiosis. *Compare* **procollagen**.

protoheme *or (esp. Brit.)* **protohaem** the iron–porphyrin prosthetic group of the **cytochromes *b***.

protohemin *see* **hemin**.

protokaryon *an obsolete term for* **prokaryon**.

protokaryote *an obsolete term for* **prokaryote**.

protolysosome *see* **primary lysosome**.

protomer any of the subunits of an oligomeric protein that are identical. *See also* **monomer**, **oligomer**. —**protomeric** *adj.*

proton **1** *symbol*: $^{1}H^{+}$; the cation derived from an atom of **protium**; a hydrogen ion of nucleon number unity; used in this sense especially when distinction between $^{1}H^{+}$, $^{2}H^{+}$ (i.e. deuteron), and $^{3}H^{+}$ (i.e. triton) is needed; any solvated species is included. **2** *symbol*: H^{+}; *commonly used term for* the cation derived from any atom of natural **hydrogen** (of which a small proportion is **deuterium**) by loss of its orbital electron; any solvated species is included. *See also* **hydrogen ion**, **hydron**. **3** *symbol*: p; a nuclear particle of nucleon number unity, having a charge equal and opposite to that of an **electron** and having a mass of 1.007 276 470 (12) Da. —**protonic** *adj.*.

proton magnetic resonance *abbr.*: PMR *or* pmr; *see* **nuclear magnetic resonance spectroscopy**.

proton magnetogyric ratio *symbol*: γ_p; a fundamental physical constant, of value 2.675 221 28(81) $\times 10^{8}$ s^{-1} T^{-1}. *See also* **gyromagnetic ratio**.

protonmotive indicating, or related to an ability to transport protons (i.e. hydrons).

protonmotive Q cycle a hypothetical mechanism put forward to explain the **protonmotive** and **redox** properties of certain components of the **respiratory chain** in the **coupling membrane** of bacteria, mitochondria, and chloroplasts. The **Q cycle** applies to the part of the respiratory chain involving passage of electrons through cytochrome *b*. Essentially, the cycle accepts two hydride ions from a reduced flavoprotein (e.g. of complex I or complex II of the respiratory chain; *see* **complex I**, **II**, **III**, **IV**) passes electrons singly to cytochrome c_1 and releases the two hydrons to the intermembrane space. **Ubiquinone** is the molecule that accepts the hydride ions, and releases the electrons and hydrons. Cytochromes b_{566} and b_{562} are involved in shuttling electrons between different oxidation states of ubiquinone during the cycle. The property of ubiquinone that it can exist as a **semiquinone** is important in the switch from two-electron to one-electron transfer.

proton number *or* **atomic number** *symbol*: Z; a dimensionless physical quantity, with a unique integral value for each chemical element, that is equal to the number of protons contained in the nucleus of each atom of the element irrespective of the mass of any particular atom. It also is equal to the number of unit positive charges on the nucleus of each atom of a given chemical element, to the number of orbital electrons surrounding the nucleus of an un-ionized atom of that element, and, for a specific nuclide of that element, to the arithmetical difference between the nuclide's **nucleon number**, A, and its **neutron number**, N; i.e. $Z = N - A$. The proton number of an element determines the position of the element in the periodic

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table. It may be attached to the symbol for the element as a left subscript, e.g. $_6$C.

proton pump *another term (esp. in pharmacology) for* **hydrogen-ion pump**.

proton relaxation enhancement *abbr.*: PRE; a technique that yields information concerning (macro)molecular motion. It depends on the enhancement of the solvent water-proton relaxation rates on addition of a macromolecule.

protooncogene a normal gene, usually concerned with the regulation of cell proliferation, that can be converted into a cancer-promoting **oncogene** by mutation. For example, in the case of the Rous sarcoma virus the viral oncogene is v-*src* (*see* ***src***). This is closely related to a normal gene, c-*src*. The appearance of v-*src* is believed to have followed the acquisition of a copy of c-*src* by an ancestor of the Rous sarcoma virus. Through many generations this ancestral gene was mutated and became dominant. Protooncogenes encode proteins involved in all aspects of controlling cell proliferation, including growth factors, growth-factor receptors, nuclear factors regulating gene expression proteins that generate second messengers, and protein kinases.

protoplasm the living contents of a cell; i.e. the matter contained within (and including) the plasma membrane, usually taken to exclude large vacuoles and masses of secretory or ingested material. In eukaryotes it includes the **nucleus** and **cytoplasm**.

protoplast a spherical, osmotically sensitive plant cell without its cell wall but retaining an intact cell membrane. The cell wall is degraded by digestion with different hydrolytic enzymes, as a mixture or sequentially, e.g. cellulase, hemicellulase. Protoplasts are used to create hybrid cells via protoplast fusion. In some cases they are totipotent, and are thus capable of yielding plants. Such protoplasts can be used in plant transformation.

protoporphyrin IX the specific substrate for the enzyme **ferrochelatase**, which catalyses the insertion of iron to form **protoheme**. It is also probably the substrate for the insertion of magnesium in the formation of chlorophylls in plants.

prototroph any strain of a microorganism (alga, bacterium, or fungus) that does not require any substances in its nutrition additional to those required by the wild type. *Compare* **auxotroph**. —**prototrophic** *adj.*

Protozoa a phylum or subkingdom comprising single-celled eukaryotic microscopic organisms, usually classified as animals. *Compare* **Metazoa**, **Parazoa**.

provirus a virus, e.g. a **retrovirus**, that is integrated into the chromosome of its host cell and can be transmitted through the generations without causing lysis of the host cell.

provitamin a compound which is converted to an active vitamin in the body. In practice the term is only applied to **carotenes**.

Pro-X dipeptidase EC 3.4.13.8; *recommended name:* prolinase; *other names*: prolyl dipeptidase; iminodipeptidase; prolinase; L-prolylglycine dipeptidase; an enzyme that catalyses the hydrolysis of Pro-|-Xaa dipeptides. It also acts on hydroxyprolyl analogues.

proximal protein any protein that binds early in the assembly of complex structures, such as ribosomes. Their presence in the partially assembled structure is required for the binding of **distal proteins**.

proximate carcinogen *or* **proximate carcinogenic metabolite** any metabolite of a **chemical carcinogen** that is itself carcinogenic; the term may embrace **ultimate carcinogen**.

Prozac *see* **fluoxetine**.

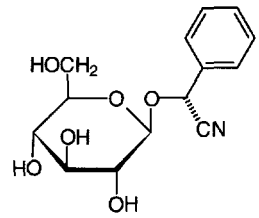
PrP *abbr. for* prion protein.

PRP protein *abbr. for* **pre-mRNA processing protein**.

PRPP *abbr. (not recommended) for* phosphoribosyl pyrophosphate (*see* **(5-)phospho(-α-D-)ribosyl diphosphate**).

PRPP synthetase *another name for* **ribose-phosphate pyrophosphokinase**.

prunasin (–)-(*R*)-mandelonitrile β-D-glucoside; a **cyanogenic** glycoside.



prunasin

ps *symbol for* picosecond.

P-selectin *see* **selectin**.

pseudoalkaloid any **alkaloid** in which the skeleton is partly derived from a terpene.

pseudoallele any of two (or more) mutations that are allelic functionally but not structurally. *See* **allele**.

pseudoaxial *(in chemistry) abbr.*: a′; *see* **conformation**.

pseudocholinesterase EC 3.1.1.8; *recommended name*: cholinesterase; *other name*: choline esterase II. An enzyme, found in blood and other tissues, that catalyses the hydrolysis of a variety of choline esters and a few other compounds. *Compare* **acetylcholinesterase**.

pseudoequatorial *(in chemistry) abbr.*: e′; *see* **conformation**.

pseudoexon a portion of an **exon** that is duplicated in an adjacent **intron**.

pseudogene *symbol*: ψ; a sequence in DNA that is related to a functional gene but cannot be transcribed. This may be due to mutational changes that preclude it from being expressed in the form of functional products or the lack of some flanking control region in the promoter. Pseudogenes may or may not contain the introns of the functional gene. Examples include pseudogenes for α, β, and ζ globulins in several species, V_κ chains of immunoglobulins, actin, and tubulin. **Processed pseudogenes**, or LINES (*see* **LINE**), occur in a genome somewhere other than the normal position of the corresponding functional gene and so cannot be expressed because of alterations in regulatory DNA sequences, or coding sequences, or both.

pseudoglobulin a globulin that is soluble in solutions of low ionic strength or in pure water. *Compare* **euglobulin**.

pseudointron an **intron** that contains 5′ and 3′ splice sites that are appropriate but not utilized in the excision of the intron.

pseudoisoenzyme any one of the epigenetically derived multiple forms of an enzyme.

pseudo-operator a functional **operator** element within a structural protein-coding region of DNA.

pseudopepsin *see* **pepsinogen**.

pseudoplasmodium *see* ***Dictyostelium discoideum***.

pseudopodium (*pl.* **pseudopodia**) a temporary protrusion or retractile process of a cell, associated with flowing movements of the protoplasm and serving for locomotion and feeding. —**pseudopodial** *adj.*

pseudouridine *symbol*: Ψ; 5-β-D-ribofuranosyluracil; a component of **transfer RNA** (tRNA) containing a C–C bond between the ribose (C-1) and uracil (C-5). Typical of the **minor nucleosides** present in tRNA, it is formed by modification of uridine in the original transcript; the chemistry of this process is unclear. When peudouridine occurs in the anticodon of transfer RNA it base pairs with adenine. *Compare* **uridine**.

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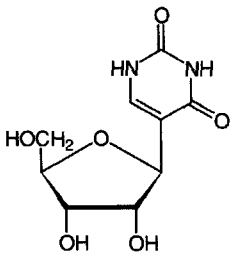


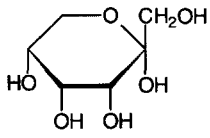
pseudouridine

psi 1 *symbol*: ψ (lower case) *or* Ψ (upper case); the twenty-third letter of the Greek alphabet. For uses *see* **Appendix A. 2** *or* **p.s.i.** *abbr. for* pounds per square inch (a unit of pressure in the Imperial and US systems of units).

PSI *abbr. for* photosystem I (*see* **photosystem**).

psicofuranine 6-amino-9-D-psicofuranosylpurine; an antibiotic produced by *Streptomyces hygroscopicus*, found to have antitumour activity. *See also* **D-psicose**.

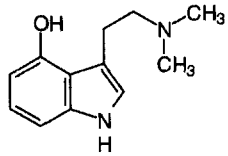
D-psicose *a nonsystematic name for* the keto-hexose D-*ribo*-2-hexulose. The hydroxyl at C-3 has the opposite configuration to that of D-fructose. It is a component of **psicofuranine**.



α-D-pyranose form

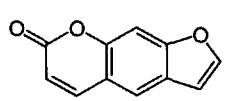
PSII *abbr. for* photosystem II (*see* **photosystem**).

psilocin 3-[2-(dimethylamino)ethyl]-1*H*-indol-4-ol; a hallucinogenic alkaloid extracted from the mushroom *Psilocybe mexicana*.



P-site *abbr. for* a peptidyl-tRNA binding site of **ribosome**; in bacteria this involves the **ribosomal proteins** L2, L14, L18, L24, L27, and L33, and a region close to the 3′ end of 16S rRNA.

psoralen 6-hydroxy-5-benzofuranacrylic acid δ-lactone; a furocoumarin present as a **phytoalexin** in many plants. It has photosensitizing and phototoxic effects in humans and animals, and is used in photochemistry, intercalating into DNA and forming cross-links on irradiation. *See also* **methoxypsoralen**.



PSP *abbr. for* pancreatic stone protein (*see* **pancreatic thread protein**).

psychosine 1-*O*-β-D-galactosylsphingosine; it is formed from UDPgalactose and sphingosine by sphingosine β-galactosyltransferase, EC 2.4.1.23. It is acylated to a cerebroside by reaction with a long-chain acyl-CoA.

psychrometer *or* **wet-and-dry bulb hygrometer** a type of hygrometer consisting of two thermometers, one with a wet bulb and one with a dry bulb. The cooling effect of evaporation from the wet bulb creates a temperature difference between the two thermometers, from which the relative humidity can be calculated.

psychrophile an organism that grows best at low temperatures (below about 20 °C). —**psychrophilic** *adj.*

P system a system of blood groups in which the antigenic determinants are oligosaccharides. The antigens are detected on erythrocytes, erythroblasts, platelets, megakaryocytes, fibroblasts, and endothelial cells; they are designated P^k, P, and P_1. The common phenotypes are P_1 (antigens P_1 and P positive) and P_2 (P antigen positive); P^k phenotypes are rare. Individuals with the p phenotype lack all of the above determinants, having only the core structure lactosylceramide, and have anti-P and anti-P^k antibodies. The determinants are:

P^k (Gb_3Cer): Gal(α1-4)Gal(β1-4)GlcCer
P (Gb_4Cer): GalNAc(β1-3)Gal(α1-4)Gal(β1-4)GlcCer
P_1: Gal(α1-4)Gal(β1-4)GlcNAc(β1-3)Gal(β1-4)GlcCer.

Pt *symbol for* platinum.

PTA *abbr. for* plasma thromboplastin antecedent (i.e. factor XI); *see* **blood coagulation**.

PTC *abbr. for* **1** plasma thromboplastin component (i.e. factor IX); *see* **blood coagulation**. **2** phenylthiocarbamoyl.

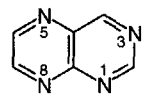
Ptd *symbol for* the phosphatidyl group.

PtdIns *symbol for* phosphatidylinositol.

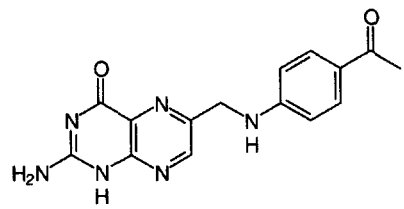
PtdIns4*P* *or* **PtdIns-4-*P*** *symbol for* phosphatidylinositol 4-phosphate.

PtdIns(4,5)P_2 *or* **PtdIns-4,5-P_2** *symbol for* phosphatidylinositol 4,5-bisphosphate.

pteridine pyrazino[2,3-*d*]pyrimidine; the parent structure of pterins and the **pteroyl** group. *See also* **xanthopterin**.



pteroyl 4-[[(2-amino-1,4-dihydro-4-oxo-6-pteridinyl)methyl]-amino]benzoyl; the acyl group of pteroic acid, and the structural basis of **folate** and its derivatives.



PTFE *abbr. for* polytetrafluoroethylene.

PTH *abbr. for* **1** parathyroid hormone (i.e. **parathyrin**). **2** phenylthiohydantoin; as in PTH-amino acid (i.e. the phenylhydantoin derivative of an amino acid).

PTI *abbr. for* pancreatic trypsin inhibitor.

PTM *abbr. for* post-translational modification.

PTS *abbr. for* phospho*enol*pyruvate-dependent sugar phosphotransferase system.

ptyalin a substance in saliva, identified as **α-amylase**.

Pu *symbol for* plutonium.

pUC vector any of a series of plasmid **cloning vectors** having an

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ampicillin resistance gene and part of the *lacZ* gene containing multiple cloning sites (MCSs). Different members of the series (e.g. pUC18, pUC19) vary in the restriction enzyme recognition sites included in the MCS. They are high copy number plasmids and so can be purified by rapid, small-scale methods of isolation. A related series of bacteriophage M13 vectors, the M13mp vectors, contain the same MCS and are useful for DNA sequencing. *See also* **Messing vector**.

PUFA *abbr. for* polyunsaturated fatty acid.

puff any discrete, localized expansion occurring at specific sites in polytene chromosomes, e.g. the giant salivary gland chromosomes in Diptera. Typically a few micrometres long, they are believed to be a gene or group of genes that are actively synthesizing RNA, which accounts for a considerable part of the mass of the puff. *See also* **Balbiani ring**.

'pull' model *a nickname for* the **Monod–Wyman–Changeux model** (for ligand-induced changes in protein conformation) because, in this model, ligands influence the equilibrium between enzyme states by sequestering the enzyme in ligand-bound forms. *Compare* **'push' model**.

pullulan an extracellular **glucan** elaborated by *Aureobasidium pullulans* (yeast form) and formed by other fungi. It is a linear structure with both (1→4)-α-D- and (1→6)-α-D-linkages. Pullulan is used as a non-caloric material, a water-retention agent, and as a film and fibre former.

pullulanase **1 isopullulanase** EC 3.2.1.57; an enzyme that catalyses the hydrolysis of **pullulan** to isopanose (i.e. 6-α-maltosylglucose). **2 neopullulanase** EC 3.2.1.135; an enzyme that catalyses the hydrolysis of pullulan to panose (i.e. 6-α-D-glucosylmaltose). **3** *see* **α-dextrin endo-1,6-α-glucosidase**.

pulsed field gel electrophoresis *abbr.*: PFGE; a type of **gel electrophoresis** in which large fragments of DNA can be separated by continuously altering the angle at which the electric current is applied.

pulse radiolysis a technique whereby reactive chemical species are generated by pulses of high-energy radiation and the subsequent reactions of these species are followed spectrophotometrically as a function of time.

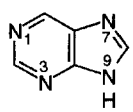
pump *(in cell biology)* any transmembrane protein that drives the active transport of ions and small molecules across the lipid bilayer. *See also* **hydrogen-ion pump**, **sodium pump**.

PUMP-1 *see* **matrilysin**.

pump-1 protease *see* **matrilysin**.

Purcell, Edward Mills (1912–97), US electrical engineer, physicist, and radioastronomer notable for his discovery (independently of F. Bloch) of the phenomenon of nuclear magnetic resonance of certain atomic nuclei and for being the first to report detection of the emission of 1420-Hz microwave radiation by interstellar dihydrogen; Nobel Laureate in Physics (1952) jointly with F. Bloch 'for their development of new methods for nuclear magnetic precision measurements and discoveries in connection therewith'.

purine **1** 1*H*-purine; 7*H*-imidazo[4,5-*d*]pyrimidine; an organic nitrogenous base, sparingly soluble in water. **2** any of a class of derivatives of 1*H*-purine; these form one of the two classes of nitrogen-containing ring compounds found in DNA and RNA, which include **adenine** and **guanine**. *See also* **purine biosynthesis**.



purine biosynthesis the biosynthesis of purine ribonucleotides. The pathway for the synthesis of purine ribonucleotides begins with the formation of 5-phospho-α-D-ribosyl diphosphate (5-phosphoribosyl-α-D-pyrophosphate, *common abbr.*: PRPP) by ribose-phosphate pyrophosphokinase, EC 2.7.6.1. This is converted to β-5-phosphoribosylamine (I) by reaction with glutamine, catalysed by amidophosphoribosyltransferase, EC 2.4.2.14; reaction of I with glycine, with hydrolysis of ATP to ADP and P_i, catalysed by **phosphoribosylamine–glycine ligase**, EC 6.3.4.13 (glycinamide ribonucleotide synthetase, *common abbr.*: GAR synthetase), brings about the formation of N^1-(5-phospho-D-ribosyl)glycinamide (II, glycinamide ribotide, *common abbr.*: GAR); II reacts with 10-formyltetrahydrofolate to form 5′-phosphoribosyl-*N*-formylglycinamide (III, *common abbr.*: FGAR), the enzyme being **phosphoribosylglycinamide formyltransferase**, EC 2.1.2.2 (GAR transformylase); III is converted to 5′-phosphoribosylformylglycinamidine (IV, formylglycinamidine ribotide, *common abbr.*: FGAM) by **phosphoribosylformylglycinamidine synthase**, EC 6.3.5.3 (*common abbr.*: FGAM synthetase) by reaction with glutamine with ATP hydrolysis to ADP and P_i. IV is converted to 1-(5-phosphoribosyl)-5-aminoimidazole (V, 5-aminoimidazole ribotide, *common abbr.*: AIR), with hydrolysis of ATP to ADP and P_i, by **phosphoribosylformylglycinamidine cyclo-ligase**, EC 6.3.3.1 (*common abbr.*: AIR synthetase); V is carboxylated to 1-(5-phosphoribosyl)-5-amino-4-imidazolecarboxylate (VI, carboxyaminoimidazole carboxamide, *common abbr.*: CAIR), by **phosphoribosylaminoimidazole carboxylase**, EC 4.1.1.21 (*common abbr.*: AIR carboxylase); VI reacts with L-aspartate, with hydrolysis of ATP to ADP and P_i, to form 1-(5-phosphoribosyl)-5-amino-4-(*N*-succinocarboxamide)-imidazole (VII, 4-(*N*-succinylocarboxamide)-aminoimidazole ribotide, *common abbr.*: SACAIR) catalysed by **phosphoribosylaminoimidazolesuccinocarboxamide synthase**, EC 6.3.2.6 (*common abbr.*: SACAIR synthetase); VII is converted, with loss of fumarate, to 1-(5-phosphoribosyl)-4-carboxamide-5-aminoimidazole (VIII, aminoimidazolecarboxamide ribotide, *common abbr.*: AICAR) by adenylosuccinate lyase, EC 4.3.2.2 (VII is an alternative substrate for this enzyme); VIII reacts with 10-formyltetrahydrofolate to form 5′-phosphoribosyl-5-formamido-4-imidazolecarboxamide (IX, formaminoimidazolecarboxamide ribotide, *common abbr.*: FAICAR), catalysed by **phosphoribosylaminoimidazolecarboxamide formyltransferase**, EC 2.1.2.3 (*common abbr.*: AICAR transformylase); IX undergoes ring closure catalysed by IMP cyclohydrolase, EC 3.5.4.10, to form inosine monophosphate (IMP), from which other purine nucleoside monophosphates are formed. Thus it is converted to AMP via adenylosuccinate, in steps catalysed by adenylosuccinate synthase, EC 6.3.4.4, and adenylosuccinate lyase, EC 4.3.2.2. It is converted to GMP via xanthosine monophosphate, in steps catalysed by **IMP dehydrogenase**, EC 1.1.1.205, and **GMP synthase**, EC 6.3.4.1. A **salvage pathway** also exists, that reconverts purine bases released during nucleic-acid degradation to nucleoside monophosphates. The enzymes adenine phosphoribosyltransferase and hypoxanthine–guanine phosphoribosyltransferase are responsible for these reactions.

purine-nucleoside phosphorylase *abbr.*: PNP; EC 2.4.2.1; *systematic name*: purine-nucleoside:orthophosphate ribosyltransferase; *other name*: inosine phosphorylase. An enzyme that catalyses the phosphorylysis of a purine nucleoside to a purine and α-D-ribose 1-phosphate. It functions in the degradation of purines; decreased activity leads to accumulation of dGTP, which affects DNA replication. Enzyme deficiency is associated with moderate immunodeficiency. Example from *Escherichia coli*, homohexamer: database code DEOD_ECOLI, 238 amino acids (25.79 kDa).

purinergic describing a type of nerve in which synaptic transmission is brought about by purine-like transmitter substances. *See* **purinoceptor**. *Compare* **adrenergic**, **cholinergic**.

purinoceptor *or* **purinergic receptor** a family of receptors (P_1, P_{2X}, P_{2Y}, P_{2Z}, P_{2T}, and P_{2U}) classified according to the relative potency of purine nucleotides – ATP, ADP, AMP, and UTP – in stimulating them and by their response to either adenosine (P_1) or ATP (P_2). P_{2Y} and P_{2U} have seven transmembrane domains and regulate turnover of phosphoinositides; example of

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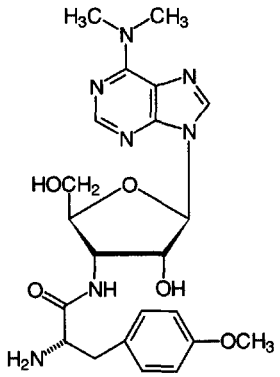
P_{2U} from *Rattus norvegicus*: database code P2UR_RAT, 374 amino acids (42.26 kDa). P_{2X}, P_{2Z}, and P_{2T} modulate the opening of an intrinsic cation channel but P_{2T} also stimulates release of intracellular Ca^{2+} and reduces synthesis of cyclic AMP. Example of P_{2X} from *R. norvegicus*: database code P2X1_RAT, 472 amino acids (52.62 kDa).

puromycin a nucleoside antibiotic produced by the soil actinomycete *Streptomyces alboniger*. It interrupts protein synthesis by virtue of its structural similarity to the 3′ end of aminoacyl-tRNA: it enters the A-site (*see* **aminoacyl site**) on the ribosome, and is incorporated into the growing polypeptide chain, thereby causing premature release of the puromycinyl polypeptide from the ribosome.



purothionin any of a group of basic peptides, isolated from grain and of $M_r \approx 5000$, that contain a large number of cysteine residues and are toxic to bacteria and fungi by inhibiting DNA transcription and RNA translation. Example purothionin γ-1 from *Triticum aestivum*: database code THG1_WHEAT, 47 amino acids (5.24 kDa).

purple membrane part of the cell membrane of *Halobacterium halobium* containing **bacteriorhodopsin**.

'push' model *a nickname for* the **Koshland model** (for ligand-induced changes in protein conformation) because, in this model, binding of the ligands results in a conformational change and does not simply select a pre-existing state. *Compare* **'pull model'**.

putidaredoxin a ferredoxin, isolated from *Pseudomonas putida*, that is an electron carrier in a hydroxylase system acting on camphor and closely related monoterpenes. *Compare* **adrenodoxin**.

putrescine 1,4-diaminobutane; the polyamine formed by decarboxylation of **ornithine** and the metabolic precursor of **spermidine** and **spermine**.

PVA *abbr. for* **1** polyvinyl alcohol. **2** polyvinyl acetate.

PVC *abbr. for* polyvinyl chloride.

PVP *abbr. for* polyvinyl pyrrolidone.

PWM *abbr. for* pokeweed mitogen.

pycnometer an apparatus for measuring the density of liquids, and also sometimes of solids. It consists of a container whose volume can be accurately measured, and that can be filled with great precision, so that when filled with the liquid in question it can be weighed to determine the density. —**pycnometric** *adj.*

Pyd *symbol for* a residue of an unspecified pyrimidine nucleoside (alternative to Y).

pyr-1 the symbol for the pyrimidine 1 gene, which encodes **CAD protein** in several eukaryotes.

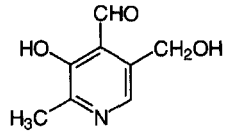
pyran *the trivial name for* either of the hypothetical isomers α-pyran, 2*H*-pyran, oxacyclohexa-3,5-diene, or γ-pyran, 4*H*-pyran, oxacyclohexa-2,5-diene, C_5H_6O. These pyrans are not known as such, but are the parent structures of various known pyranoid compounds such as dihydropyran, α- and γ-pyrones, and pyranoses.

pyranoid pyran-like, i.e. describing a molecular structure that consists of or contains a ring of five carbon atoms and one oxygen atom (as in **pyran**).

pyranose *symbol*: *p*; any monosaccharide or monosaccharide derivative whose molecule contains a **pyranoid** ring. *Compare* **furanose, septanose**.

pyridine-nucleotide coenzyme any of a group of coenzymes containing a nicotinamide nucleotide residue, e.g. nicotinamide-adenine dinucleotide (NAD^+); now known as **nicotinamide-nucleotide coenzymes**.

pyridoxal *abbr.*: PL; 3-hydroxy-5-(hydroxymethyl)-2-methyl-4-pyridine carboxaldehyde; a compound with **vitamin B_6** activity.



pyridoxal kinase EC 2.7.1.35; an enzyme that catalyses the formation of pyridoxal 5′-phosphate from ATP and pyridoxal with release of ADP. Example (fragment) from sheep: database code A61483, 11 amino acids (1.24 kDa).

pyrimidine **1** 1,3-diazine; an organic nitrogenous base, sparingly soluble in water. **2** any of a class of derivatives of pyrimidine (def. 1); these form one of the two categories of nitrogen-containing ring compounds found in DNA and RNA, which include **cytosine**, **thymine**, and **uracil**. *See also* **pyrimidine biosynthesis**.

pyrimidine biosynthesis *or* **pyrimidine ribonucleotide biosynthesis** pyrimidines are formed from carbamoyl phosphate (*see* **carbamoyl-phosphate synthase**) after conversion to carbamoyl aspartate in a reaction with L-aspartate catalysed by **aspartate transcarbamylase**, EC 2.1.3.2. Carbamoyl aspartate is converted to orotate via dihydroorotate, in steps catalysed by **dihydroorotase**, EC 3.5.2.3, and dihydroorotate dehydrogenase, EC 1.3.99.11. Orotate is phosphorylated to orotidine monophosphate (OMP) in a reaction with 5-phospho-α-D-ribosyl diphosphate catalysed by **orotate phosphoribosyltransferase**, EC 2.4.2.10. OMP is converted to uridine monophosphate by **orotidine 5′-phosphate decarboxylase**, EC 4.1.1.23.

pyrimidine dimer any structure formed within a strand of DNA from two neighbouring pyrimidine residues through covalent cross-linking induced by ultraviolet irradiation. Two types are known. (1) Addition of one pyrimidine ring to the other at each end of their respective 5,6-double bonds generates a **cyclobutadipyrimidine**, a fully substituted cyclobutane. Such a dimer is formed most readily from two thymine residues (*see* **thymine dimer**), but may be formed also from two cytosine residues, or from one cytosine and one thymine residue. For each of these varieties there are four possible configurational isomers: if the pyrimidine rings have become linked in a parallel manner, i.e. by 5–5′ and 6–6′ bonds, the configuration is designated by the prefix *syn*-, but if they are linked in an antiparallel manner, i.e. by 5–6′ and 6–5′ bonds, it is designated by *anti*-; further, if the pyrimidine rings are both on the same side of the plane of the cyclobutane ring, the dimer is described as being in the '**doghouse configuration**', designated by the prefix *cis*-, but if the rings are on opposite sides of the cyclobutane plane, the dimer is said to be in the '**chair configuration**', designated by *trans*-. The presence of a

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cyclobutadipyrimidine in a DNA strand causes a local distortion of the DNA duplex and blocks the action of DNA polymerase, thus preventing replication; cell death may ensue unless repair is effected by **photoreactivation**. (2) Alternatively, addition may take place between position 6 of one pyrimidine residue and position 4 of an adjacent one, with creation of a single covalent link and generation of a **(6–4)photoproduct**. Such a dimer is usually formed between position 6 of a cytosine or thymine residue on the 5′ side of a dinucleotide segment and position 4 of a cytosine residue on its 3′ side. The (6–4)photoproduct is thought to be the main type of lesion in DNA responsible for mutations; it is not susceptible to photoreactivation, but can be eliminated by other DNA-repair mechanisms, e.g. **excision repair**.

pyrimidine-nucleoside phosphorylase any of several enzymes that function in the catabolism of pyrimidines; examples are: (1) **Uridine phosphorylase**, EC 2.4.2.3; it catalyses the phosphorolysis of uridine to uracil and α-D-ribose 1-phosphate. Example from *Escherichia coli*, homohexamer showing 4-, 6-, and 8-fold symmetry: database code UDP_ECOLI, 252 amino acids (27.00 kDa). (2) **Thymidine phosphorylase**, EC 2.4.2.4; it catalyses the phosphorylysis of thymidine to thymine and 2-deoxy-D-ribose 1-phosphate. Example from *E. coli*, homodimer: database code DEOA_ECOLI, 441 amino acids (47.28 kDa).

pyro+ *or (before a vowel)* **pyr+** *comb. form* **1** of, relating to, caused, or produced by fire. **2** *(in chemistry)* indicating material derived by the action of heat; it often indicates an acid formed by loss of a molecule of water in a heating process, and hence also some anhydrides, e.g. pyrophosphate.

pyrocatechol *or* **pyrocatechin** *or (formerly)* **catechol** 1,2-benzenediol; *o*-dihydroxybenzene. *Compare* **catecholamine**, ***o*-benzoquinone**, **hydroquinone**.

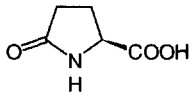
pyrolysis the decomposition or dissociation of a chemical compound by the application of heat. *See also* **thermolysis**. —**pyrolytic** *adj.*; **pyrolyse** *or (sometimes, US)* **pyrolyze** *vb.*

pyrophosphatase **1** *an imprecise name for* **inorganic pyrophosphatase**. **2** *the generic name for* any of a number of the enzymes within sub-subclass EC 3.6.1 (enzymes acting on diphosphate bonds); e.g. ATP pyrophosphatase (EC 3.6.1.8).

pyrophosphate *an older name for* **diphosphate** (def. 1–5) (use no longer recommended although it is still used as an alternative in such terms as inorganic pyrophosphate, pyrophosphatase, etc.). *See also* **inorganic diphosphate**.

pyrophosphokinase *the general name for* any enzyme belonging to the sub-subclass EC 2.7.6, diphosphotransferases, which transfer a diphosphate group from ATP to a named substrate; e.g. GTP pyrophosphokinase (EC 2.7.6.5), which converts guanosine 5′-triphosphate, GTP to guanosine 3′-phosphate 5′-triphosphate, pppGpp.

pyrrolidonecarboxylic acid *symbol*: <Glp; pyroglutamic acid; 5-oxoproline; pyrrolid-2-one-5-carboxylic acid.



L-form

1-pyrroline-5-carboxylate dehydrogenase EC 1.5.1.12; an enzyme that catalyses a reaction between 1-pyrroline-5-carboxylate (*abbr.*: P5C), NAD^+, and H_2O to form L-glutamate and NADH. P5C is an intermediate in the conversion of glutamate, proline, and ornithine. Example from *Escherichia coli*, a bifunctional protein that also has **proline dehydrogenase** activity: database code PUTA_ECOLI, 1320 amino acids (143.66 kDa).

pyrroloquinoline–quinone *abbr.*: PQQ; *an alternative name for* **methoxatin**.

pyruvate *trivial name for* 2-oxopropanoate, CH_3COCOO^-; it is found in virtually every type of cell and species, being an important intermediate in many pathways including the catabolism of glucose, and the biosynthesis of amino acids and carbohydrates.

pyruvate carboxylase *abbr.*: PCB; EC 6.4.1.1; *systematic name*: pyruvate:carbon dioxide ligase (ADP-forming); *other name*: pyruvic carboxylase; an enzyme that catalyses a reaction between ATP, pyruvate, and HCO_3^- to form oxaloacetate, ADP, and orthophosphate; biotin and manganese or zinc are cofactors. Example from yeast (PCB1) homotetramer: database code PYC1_YEAST, 1178 amino acids (129.95 kDa).

pyruvate decarboxylase EC 4.1.1.1; *systematic name*: 2-oxo-acid carboxy-lyase; *other names*: α-carboxylase, pyruvic decaboxylase; α-ketoacid carboxylase. An enzyme that catalyses the decarboxylation of a 2-oxo acid to an aldehyde and CO_2; thiamine diphosphate is a coenzyme. Example from yeast (there are three related isozymes), homotetramers, isozyme 1: database code DCP1_YEAST, 563 amino acids (61.44 kDa).

pyruvate decarboxylase kinase *or* **pyruvate dehydrogenase kinase** a subunit of the mammalian **pyruvate dehydrogenase complex**. It phosphorylates three serine residues on pyruvate dehydrogenase (lipoamide) resulting in loss of activity, and is stimulated by elevated levels of acetyl-CoA and NADH.

pyruvate dehydrogenase complex an enzyme complex that catalyses the overall reaction between pyruvate, NAD^+, and coenzyme A to form acetyl-CoA, NADH, and CO_2. The complex consists of three activities: (1) **pyruvate dehydrogenase (lipoamide)**, designated E_1, catalysing a reaction between pyruvate and lipoamide to form *S*-acetyldihydrolipoamide and CO_2; (2) **dihydrolipoamide *S*-acetyltransferase**, designated E_2, catalysing a reaction between *S*-acetyldihydrolipoamide and coenzyme A to form acetyl-CoA and dihydrolipoamide; and (3) **dihydrolipoamide dehydrogenase**, designated E_3, which oxidizes dihydrolipoamide to lipoamide. The complex is regulated by the phosphorylation and dephosphorylation of the pyruvate dehydrogenase (lipoamide) component, phosphorylation being catalysed by **pyruvate decarboxylase kinase** and removal of phosphate being catalysed by **[pyruvate dehydrogenase (lipoamide)] phosphatase** (or pyruvate decarboxylase phosphatase), EC 3.1.3.43. Elevated levels of NADH and acetyl-CoA inhibit the complex by stimulating the kinase.

pyruvate dehydrogenase (lipoamide) EC 1.2.4.1; *systematic name*: pyruvate:lipoamide 2-oxidoreductase (decarboxylating and acceptor-acetylating); *other names*: pyruvate decarboxylase; pyruvate dehydrogenase; pyruvic dehydrogenase. A component enzyme of the **pyruvate dehydrogenase complex**. It catalyses a reaction between pyruvate and lipoamide to form *S*-acetyldihydrolipoamide and CO_2; thiamine diphosphate is a coenzyme. Example, pyruvate dehydrogenase E_1 component from *Escherichia coli*, homodimer, flavoprotein: database code ODP1_ECOLI, 886 amino acids (99.50 kDa).

[pyruvate dehydrogenase (lipoamide)]-phosphatase EC 3.1.3.43; an enzyme that catalyses the hydrolysis of phosphate from [pyruvate dehydrogenase (lipoamide)] phosphate. This hydrolysis activates the enzyme activity. Example (precursor) from *Bos taurus*, catalytic subunit: database code PDP_BOVIN, 538 amino acids (61.12 kDa).

pyruvate kinase EC 2.7.1.40; *systematic name*: ATP:pyruvate 2-*O*-phosphotransferase; *other names*: phospho*enol*pyruvate kinase; phospho*enol* transphosphorylase. An enzyme that catalyses the formation of pyruvate and ATP from phospho*enol*pyruvate and ADP; it requires Mg^{2+} and K^+. In the glycolytic pathway, it effects the phosphorylation of ADP to ATP. In many cases the enzyme is a homotetramer. Example from yeast: database code KPYK_YEAST, 500 amino acids (54.48 kDa).

[pyruvate kinase]-phosphatase EC 3.1.3.49; an enzyme that

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catalyses the hydrolysis of phosphate from [pyruvate kinase] phosphate in order to activate pyruvate kinase.

pyruvate–malate cycle a metabolic cycle involving malate dehydrogenase (oxaloacetate-decarboxylating) (the **malic enzyme**) that occurs during fatty-acid biosynthesis. In this situation, acetyl-CoA is transported into the cytoplasm as citrate, formed by mitochondrial citrate synthase; the citrate is cleaved in the cytoplasmic compartment to acetyl-CoA, which participates in fatty-acid synthesis, and oxaloacetate. No transport system exists for taking this oxaloacetate back into the mitochondrion; however, it can be reduced to malate by cytoplasmic NAD^+-linked malate dehydrogenase, and the malate so formed can be converted to pyruvate by malic enzyme, EC 1.1.1.38; the pyruvate can then be transported into the mitochondrion, to be carboxylated to oxaloacetate by **pyruvate carboxylase**.

pyruvic–malic carboxylase *an alternative name for* **malic enzyme**.

PYY *abbr. for* peptide YY.

PZ *abbr. for* pancreozymin.

PZP *abbr. for* pregnancy zone protein.

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Qq

q *symbol for* quartet (in nuclear magnetic resonance spectroscopy).

q *symbol for* **1** heat (alternative to *Q*). **2** partition function (individual entity). **3** specific humidity.

Q *symbol for* **1** a residue of the α-amino acid L-glutamine (alternative to Gln). **2** a residue of the ribonucleoside **pseudouridine** (replacing Ψ for computer work). **3** coenzyme Q (i.e. **ubiquinone**); not recommended. The number of prenyl residues may be indicated by a suffixed arabic number, e.g. Q-10. **4** queuosine.

Q *symbol for* **1** heat (alternative to *q*). **2** electric charge. **3** radiant energy (alternative to *W*). **4** *or* Q_v quantity of light. **5** partition function (whole system).

Q_{10} *symbol for* temperature coefficient of a reaction.

Q_{CO_2} *symbol for* metabolic quotient in respect of discharge of carbon dioxide; it is expressed in terms of microlitres CO_2 evolved per milligram dry mass of material per hour.

Q_{O_2} *symbol for* metabolic quotient in respect of uptake of dioxygen; it is expressed in terms of microlitres O_2 absorbed per milligram dry mass of material per hour.

Q_S *symbol for* a measure of the activity of an enzyme, especially a respiratory enzyme, defined as the number of microlitres (at stp) of gaseous substrate S used up per hour per milligram enzyme. It could be extended to nongaseous substrates by taking 1 μmol as equivalent to 22.4 μL.

QAE *abbr. for* the quaternized aminoethyl; denoting the group diethyl-(2-hydroxypropyl)aminoethyl; $(C_2H_5)_2(CH_3{-}CHOH{-}CH_2)N^+{-}CH_2{-}CH_2{-}$; a strongly basic substituent sometimes used in hydroxylated chromatographic support matrices, as in QAE-Sephadex, to form anion exchangers. *Compare* **DEAE**.

Q cycle *an alternative name for* **protonmotive Q cycle**.

Q enzyme *an alternative name for* amylopectin branching enzyme; *see* **branching enzyme**.

Q gas a mixture of 98.7% helium and 1.3% butane, used as filling for gas-flow Geiger counters.

$QH^{\cdot}$ *symbol for* ubisemiquinone.

QH_2 *symbol for* ubiquinol.

quad denoting four kinetically important substrates or products in an enzyme mechanism. *See* **reactancy of enzymes**.

quadri+ *or (sometimes)* **quadru+** *or (before a vowel)* **quadr+** *comb. form* four; fourth or one-fourth; square.

quadruplex DNA *another name for* **tetraplex DNA**.

quality factor *or (formerly)* **relative biological effectiveness** an index of the ability of a given type of ionizing radiation to cause biological damage, depending on the density of the ionization produced relative to that produced by gamma radiation. For all X- (and gamma) radiation and beta particles (+ or –) likely to be encountered in the use of radioisotopes it is assigned a value of unity, for thermal neutrons usually a value of 3, and for all alpha particles a value of 10. *See also* **dose equivalent**.

quanta the plural of **quantum**.

quantal **1** of, pertaining to, or being a **quantum** or something that is quantized; of or pertaining to the quantum theory. **2** of a biological effect or response in which there are only two categories, conditions, or states (e.g. all or none, alive or dead). —**quantally** *adv.*

quantitative electrophoresis *(sometimes) an alternative name for* **crossed immunoelectrophoresis**.

quantity *or* **physical quantity** *(in systems of measurement)* any property whose value can be expressed as the product of a numerical value and a unit. In the International System of Units (*see* **SI**) there are seven **base quantities**, physical quantities regarded as being dimensionally independent; these are: length, mass, time, electric current, thermodynamic temperature, amount of substance, and luminous intensity; all are arbitrarily defined. **Derived units** are expressed algebraically in terms of the base units. Symbols for physical quantities are printed in italic type; they are generally single Roman or Greek letters, and may be lower case or capital.

quantity of electricity *an alternative name for* **electric charge**.

quantize *or* **quantise** to restrict (a physical quantity) to a set of discrete values, characterized by quantum numbers. A quantized physical quantity cannot vary continuously but must change in steps. —**quantization** *or* **quantisation** *n.*

quantum (*pl.* **quanta**) **1** a (specific) quantity or amount of something. **2** a unit amount of a physical quantity, especially of electromagnetic energy, such that all other amounts are integral multiples of it. According to the **quantum theory**, a quantum of energy released during radiation emission or taken up during radiation absorption is equal to $h\nu$, where h is the Planck constant and ν the frequency of the radiation in hertz. A quantum of light (or other electromagnetic energy) is termed a **photon**.

quantum efficiency **1** *(in a luminescent system)* the fraction of the molecules in a particular excited state that emit luminescence. **2** *(in biochemistry) an alternative term for* **quantum yield** (def. 1).

quantum mechanics a mathematical theory developed from the quantum theory (*see* **quantum**) as a replacement for classical mechanics in order to explain satisfactorily the behaviour of atoms, molecules, and elementary particles in terms of observable quantities such as the intensities and frequencies of spectral lines.

quantum number any of a set of small integral or half-integral numbers that give the various possible values of a quantized property of a system. Quantum numbers are used especially in describing the properties of elementary particles, such as their charge (values of 0, +1, or –1) or spin (values of +½, or –½), and in specifying the energy states of electrons in atomic orbitals (each of which is characterized by a unique set of four quantum numbers).

quantum requirement *(in photosynthesis)* the inverse of **quantum yield** (def. 2); i.e. the number of quanta of light energy required to bring about the release of one molecule of dioxygen. The theoretical value is eight, but the value observed in an experimental system is generally somewhat higher, depending on conditions.

quantum theory *see* **quantum**.

quantum yield **1** *abbr.*: *Q*; *(in a luminescent system)* the probability of luminescence occurring in given conditions, expressed by the ratio of the number of photons, i.e. quanta of light, emitted by the luminescing species to the number absorbed. *Compare* **quantum efficiency**. The measurement of *Q* requires the counting of photons, because

$$Q = \text{photons emitted/photons absorbed.}$$

It requires highly specialized instrumentation, but a less rigorous method may be employed in which the fluorescence of a fluor is compared with that of a fluor of known *Q*. Then

$$Q_x = [I_x Q_s A_s]/[I_s A_x]$$

where Q_s is the quantum yield of the standard, I_s and I_x are the fluorescence intensities of the sample and standard and A_s and A_x are the percentage of absorption of each solution at the exciting wavelength. **2** *(in photosynthesis)* the inverse of **quantum requirement**; i.e. the fractional number of molecules of carbon dioxide reduced per photon absorbed.

quartz a colourless, often transparent, glassy form of silica, SiO_2, used in optical devices and cuvettes because of its transparency to near-ultraviolet radiation. It is enantiomorphous,

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the right- and left-handed forms rotating the plane of polarized light in opposite directions.

quaternary 1 consisting of four (items, parts, etc.); by or in fours. 2 *(in chemistry)* consisting of or containing an atom bound to four atoms or groups. 3 of the fourth order; fourth in a series or hierarchy.

quaternary ammonium compound any compound that can be regarded as derived from ammonium hydroxide or an ammonium salt by replacement of all four hydrogen atoms of the NH_4^+ ion by organic groups. Certain compounds of this class – ones in which one of the organic groups is a long-chain (C_8–C_{18}) alkyl group and the other three are shorter-chain alkyl or other groups – have the properties of cationic detergents and are powerful antimicrobial agents. They are bacteriostatic at low concentrations and bactericidal at higher concentrations, being generally more active against Gram-positive than Gram-negative organisms. They display relatively low toxicity to higher animals and humans, and hence are widely used as antiseptics and disinfectants.

quaternary structure the fourth order of complexity of structural organization exhibited by protein, nucleic acid, and nucleoprotein molecules. It refers to the arrangement in space of the subunits of a multimeric macromolecule and the ensemble of its intersubunit contacts and interactions without regard to the internal geometry of the subunits. Hence it is possessed only when the molecule in question is made up of at least two (identical or nonidentical) subunits that are (at least potentially) separable, i.e. are not linked by covalent bonds.

Quellung reaction *or* **Neufeld Quellung reaction** *or* **pneumococcus capsule swelling reaction** the swelling of the capsule observed when specific antibody is mixed with suitable bacterial cells (e.g. pneumococci). It is probably due to deposition of antibody on the outside of the capsule, making the latter clearly visible. [From the German, *Quellung*, swelling; described by Ferdinand Neufeld (1869–1945), German bacteriologist, in 1902.]

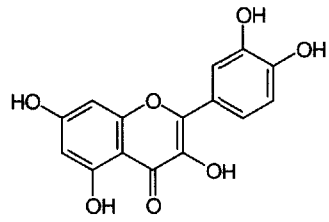
quench correction *(in liquid-scintillation counting)* a correction to be applied to an observed count rate to allow for losses resulting from **quenching** (def. 2).

quenched flow *see* **rapid-reaction kinetics**.

quencher a substance capable of reducing or destroying luminescence through deactivation of an excited chemical species. In biological systems this usually occurs by chemical reaction (e.g. complex formation), by exchange of energy on collision, or by resonance energy transfer.

quenching 1 the reduction or destruction of luminescence, especially fluorescence, of a sample by addition or inclusion of a **quencher**. Fluorescence quenching is the basis of a useful technique for studying the binding of small molecules to proteins or other macromolecules. 2 the reduction by whatever means of the efficiency of energy transfer from beta particles to the photomultiplier(s) in a liquid-scintillation counter. Such means include: (1) **dilution quenching** – reduction of the probability of scintillation occurring through dilution of the scintillator by the sample; (2) **chemical** (or **impurity**) **quenching** – absorption by a component of the sample of some of the energy of the beta particles without emitting photons, or (without fluorescing and in competition with the primary fluor) of some of the photons emitted by excited solvent molecules; and (3) **colour quenching** – absorption by a coloured component of the sample of some of the photons emitted by the secondary fluor. 3 the termination of a chemical or enzymic reaction by addition of another reagent or sudden change of the conditions.

quercetin 3,3′,4′,5,7-pentahydroxyflavone; a member of the **flavonoids**, or **flavones**, widely distributed in plants, often as **glycosides**; it is the aglycon of **quercitrin**, **rutin**, and other materials. Known in folk medicine for its anti-inflammatory properties, it inhibits the **lipoxygenase** pathway, has some antiplatelet and antithrombotic activity *in vivo*, inhibits mast-cell degranulation, and possesses anti-asthmatic activity. It inhibits many enzymes, including protein kinases, and also inhibits DNA, RNA, and protein synthesis. A number of its actions may reflect its property as a nucleoside antagonist.



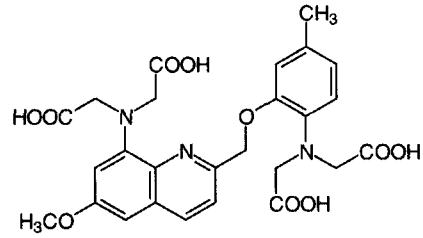
quercitrin quercetin-3-L-rhamnoside. *See also* **quercetin**.

query language very high level computer language used in interrogating databases.

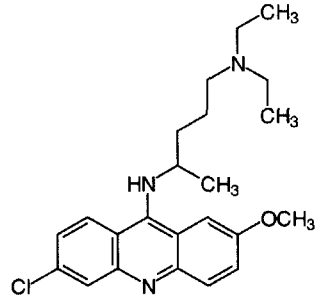
queuosine *symbol*: Q; any one of a series of nucleosides found in tRNA and having an additional pentenyl ring added via an NH group to the methyl group of 7-methylguanosine. The pentenyl ring may carry other substituents.

Qui *symbol for* a residue (or sometimes a molecule) of the deoxyaldohexose **quinovose**.

Quin-2 *abbr. for* 2-[(2-amino-5-methylphenoxy)methyl]-6-methoxy-8-aminoquinoline-*N*,*N*,*N*′,*N*′-tetraacetic acid; a molecule functionally related to the Ca^{2+}-chelating agent **EGTA**, but containing fluorescent groups. The quantum yield of fluorescence is greatly enhanced on binding Ca^{2+}, leading to its use as a quantitative indicator of Ca^{2+} concentration. It is normally used as its tetraacetoxy ester, which readily crosses the plasma membrane and is then hydrolysed within the cell by esterases to Quin-2, the polar nature of which causes it to be retained as an intracellular indicator. *See also* **Fura-2**, **INDO-1**.



quinacrine *or* **mepacrine** *or* **atebrine** 6-chloro-9-(4-diethylamino-1-methylbutylamino)-2-methoxyacridine; a derivative of **acridine**, formerly used as an antimalarial and anthelmintic. It fluoresces powerfully in UV light and can be used as a fluorochrome to label DNA in chromosomes.



quinacrine mustard a compound derived by chloro-substitution of the terminal methyls of **quinacrine** ethylamino groups, and possessing properties of an alkylating agent; this enhances its value as a DNA-labelling agent.

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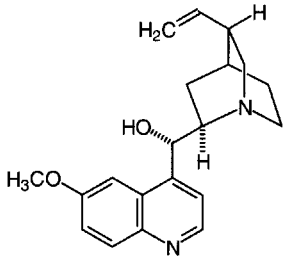
quinhydrone an addition compound of one mole each of hydroquinone and *p*-benzoquinone. It is a reddish-brown crystalline substance with a dark-green lustre, useful as an antioxidant, in photography, and as a redox system in the **quinhydrone electrode**.

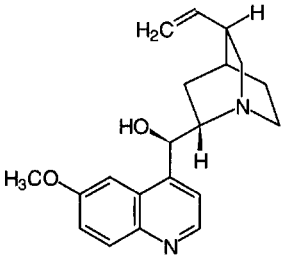
quinhydrone electrode a half-cell consisting of a bright platinum (or sometimes gold) electrode immersed in a test solution to which has been added a little **quinhydrone**. It has an electric potential related to the pH value of the solution and thus is useful as a secondary hydrogen electrode for the electrometric measurement of pH.

quinic acid the D enantiomer (1α,3α,4α,5β)-1,3,4,5-tetrahydroxycyclohexanecarboxylic acid occurs commonly in plants, either free or as esters (e.g. **chlorogenic acid**), and may make up as much as 2–10% of the dry weight of leaves. It may be formed by the **shikimate pathway**. Its catabolism to protocatechuic acid has been extensively studied in *Aspergillus nidulans* and *Neurospora crassa*.

quinidine β-quinine; 6′-methoxycinchonan-9-ol; a stereoisomer of **quinine** noted for its cardiac anti-arrhythmic effects.



quinine 6′-methoxycinchonan-9-ol; a bitter-tasting alkaloid obtained especially from the bark of cinchona, any of a number of trees or shrubs of the tropical genus *Cinchona* (especially the Javan species *C. lidgeriana* and various South



American species). It was formerly much used (and sometimes is still needed) for the prevention and treatment of malaria; it binds to the DNA of the malarial parasite, *Plasmodium* spp., and is thought thereby to inhibit biosynthesis of the parasite's nucleic acids. Quinine and drinks containing it (e.g. tonic water) help to prevent cramp. *Compare* **quinidine**.

quinoid *or* **quinonoid** of, derived from, or resembling a **quinone** (def. 2).

quinol *an alternative name for* **hydroquinone**.

4-quinolone antibiotic *a generic term for* any of a wide range of synthetic antibacterial compounds whose molecular structures contain a 4-oxo-1,4-dihydroquinoline or a 4-oxo-1,4-dihydrocinnoline nucleus; e.g. **cinoxacin**, **ciprofloxacin**, **nalidixic acid**, **oxolinic acid**. Their antibiotic activity derives from interaction with the A subunit of bacterial DNA gyrase (*see* type II **DNA topoisomerase**); this results in trapping of bacterial DNA in the complex it forms with the A sububit. Rejoining of the DNA strands broken by the enzyme is thereby arrested.

quinone **1** *a common name for* ***p*-benzoquinone**. **2** any member of a class of diketones derivable from aromatic compounds by conversion of two CH groups into CO groups with any necessary rearrangement of double bonds. Simple quinones are usually *p*-quinones, i.e. derivatives of *p*-benzoquinone (*compare* **hydroquinone** (def. 2)), but they may also be *o*-quinones, i.e. derivatives of ***o*-benzoquinone** (*compare* **catechol** (def. 2)). Naturally occurring quinones form a large, varied, and widespread group of compounds; they include numerous pigments, various electron carriers (e.g. **plastoquinone**, **ubiquinone**), and vitamins K. *See also* **semiquinone**.

+quinone *comb. form* denoting a **quinone** (def. 2); e.g. benzoquinone, anthroquinone, naphthoquinone.

quinonoid *an alternative term for* **quinoid**.

quinoprotein *a proposed name for* any of a number of bacterial oxidoreductase enzymes within the sub-subclass EC 1.1.99 that have pyrroloquinoline–quinone (*see* **methoxatin**) as coenzyme or prosthetic group. The category includes alcohol dehydrogenase (acceptor) (EC 1.1.99.8) of methylotrophic bacteria, glucose dehydrogenase (pyrroloquinoline-quinone) (EC 1.1.99.17), and a number of dehydrogenases acting on other specified (types of) alcohols or polyols.

quinovosamine 2-amino-2,6-dideoxy-D-glucose; an amino derivative of **quinovose** present in bacterial polysaccharides.

quinovose *symbol*: Qui; *a trivial name for* 6-deoxy-D-glucose. α-Quinovose occurs, e.g., as its 6-sulfo derivative (6-deoxy-α-D-glucopyranosyl 6-*C*-sulfate) in the sulfoquinovosyl diacylglycerols, which form one of the two major groups of the glycerolipids of chloroplasts. The sulfoquinovosyl derivative also occurs in some **cardiac glycosides**.

quisqualate receptor *see* **α-amino-3-hydroxy-5-methyl-isoxazole-propionic acid receptor**.

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Rr

r **1** *symbol for* **ribo+** (def. 1); it is used as a prefix in (one- or three-letter) symbols for ribonucleosides for emphasis or clarity, especially to distinguish from 2′-deoxyribonucleosides. **2** *symbol for* reaction. **3** *abbr. for* rat (as a prefix to an abbreviation for the name of a peptide hormone); denoting derived (or as if derived) from a rat or rats; e.g. rGH.

r *symbol for* **1** concentration ratio. **2** rate of concentration change. **3** radius. **4** interatomic distance.

R *symbol for* **1** a residue of the α-amino acid L-arginine (alternative to Arg). **2** a residue of an incompletely specified base in a nucleic-acid sequence that may be either adenine or guanine. **3** a residue of an unspecified purine nucleoside (alternative to Puo). **4** an unspecified univalent group in a formula of an organic compound. The group must be attached by means of carbon and derived from an aliphatic, carbocyclic, or heterocyclic compound. Up to three such groups, when different, may be designated R, R′, and R″, or R^1, R^2, and R^3; for more than three such groups, superscript numerals only should be used. **5** röntgen (a non-SI unit of radiation exposure). **6** resonance effect (in electron displacement).

R *symbol for* **1** electric resistance. **2** thermal resistance. **3** gas constant. **4** molar refraction.

R *stereochemical descriptor* denoting *rectus*; i.e. the absolute configuration of a chiral compound in which the priority (obtained using the Cahn–Ingold–Prelog sequence rules) of the substituent groups on the chiral centre decreases in a clockwise (right-handed) direction. For use as a prefix in chemical nomenclature, the descriptor is placed in parentheses and connected with a hyphen, e.g.(*R*)-alanine. For chiral compounds in which the relative but not the absolute configuration is known, *rectus* configuration is denoted by the prefix (*R**)-. *See* **sequence rule**. *Compare* ***S***.

R_B *symbol for* R_B value.

R_f *or* ***R_F*** *symbol for* R_f value.

R_p *symbol for* phosphorylation state ratio.

R_s *symbol for* saturation ratio.

RAB a gene encoding a Rab protein – any of a family of GTP-binding proteins similar to Ras proteins (*see* ***RAS***) and probably involved in membrane traffic, etc. Example, Rab-2 from human and dog (identical sequences): database code RAB2_HUMAN, 212 amino acids (23.52 kDa).

rabbit aorta-contracting substance *abbr.*: RCS; a name given (in 1969) to an unstable factor released from guinea-pig lung that caused contraction of isolated strips of rabbit aorta. The activity was probably due to the presence of thromboxane A_2 (*see* **thromboxane**).

rabbit reticulocyte system a cell-free system, from lysed rabbit reticulocytes, that translates added eukaryote mRNAs from a wide variety of heterologous sources. Endogenous mRNA is destroyed using a Ca^{2+}-dependent ribonuclease, micrococcal endonuclease; this enzyme is inactivated by adding EGTA. Heterologous mRNA is then added and is translated by the system.

rac- *abbr. for* racemo-.

RACE *abbr. for* rapid amplification of cDNA ends; a variation on the **polymerase chain reaction** designed for amplification of cDNA corresponding to low-abundance mRNA.

racemase any enzyme that interconverts the two enantiomers of a chiral compound; such enzymes are categorized in subclass EC 5.1 (which also includes **epimerases**). If more than one chiral centre is present, a racemase must invert configuration of all the chiral centres. Thus, the name methylmalonyl-CoA racemase, sometimes used for methylmalonyl-CoA epimerase (EC 5.1.99.1), is incorrect – the enzyme does not change configurations of the chiral centres of the CoA moiety.

racemate any homogeneous phase containing equimolar amounts of enantiomeric molecules.

racemic *symbol*: (±)- *or (formerly) dl-*; denoting the presence of equimolar amounts of the dextrorotatory and levorotatory enantiomers of a compound, regardless of whether the (optically inactive) product formed is crystalline, liquid, or gaseous. A homogeneous solid phase composed of equimolar amounts of enantiomeric molecules is termed a **racemic compound**, and a mixture of equimolar amounts of enantiomeric molecules present as separate solid phases is termed a **racemic mixture**; *see also* **racemate**. A (±)-product may be resolved into its (+)- and (–)-components. The term is derived from **racemic acid** [from Latin *racemus*, bunch of grapes], the optically inactive mixture of (+)- and (–)-tartaric acids sometimes found during the manufacture of wine. By extension, the term is applied to DL- and (*RS*)-mixtures. *See* **D/L convention**, **optical isomerism**, **sequence rule**. *See also* ***racemo-***.

racemize *or* **racemise** to induce the formation of a mixture of the two possible enantiomers from one of the pure isomers of a chiral compound. —**racemization** *or* **racemisation** *n.*

racemo- *abbr.*: *rac-*; *prefix (in chemical nomenclature)* designating a racemate. It may be used as an alternative to the symbol (±)- or (for certain classes of racemic compounds) the symbol DL-. *Compare* ***meso-***.

rachitic of, pertaining to, or afflicted with **rickets**.

rachitis *an alternative name for* **rickets**.

rachitogenic tending to cause **rickets**.

rad **1** *symbol for* radian. **2** *symbol*: rad *or* (to avoid possible confusion with **rad** (def. 1)) rd; the cgs unit of absorbed dose of ionizing radiation, equivalent to an absorption of 0.01 joule of energy per kilogram (= 100 ergs per gram) of irradiated material. Whereas the rad represents, in practice, about the same amount of energy as the **röntgen** (the exact equivalence depending on the material irradiated), it applies to any type of ionizing radiation in any medium. 1 rad = 0.01 Gy. **3** *abbr. for* radiation.

radial **1** of, resembling, or relating to a radius or ray; in rays. **2** emanating from the centre of a circle or a common central point. **3** spreading out uniformly in all directions on a surface. —**radially** *adv.*

radian *symbol*: rad; the SI supplementary unit of plane angle. One radian is equal to the angle subtended at the centre of a circle by an arc whose length is equal to the radius. It is dimensionless. There are 2π radians in a circle; 1 rad $\approx$ 57.295 78°.

radiant energy *symbol*: Q *or* W; the energy of any form of electromagnetic radiation. The SI derived unit is the **joule**.

radiant intensity *symbol*: I; the **radiant power** of radiation from a point source per unit of solid angle; i.e. $I = \mathrm{d}\Phi/\mathrm{d}\Omega$, where Φ is the radiant power and Ω is the solid angle measured in steradians. The SI unit is the watt per steradian (W sr^{-1}).

radiant power *or* **radiant flux** *symbol*: P *or* Φ; the rate of flow of energy of radiation; i.e. $\Phi = \mathrm{d}Q/\mathrm{d}t$, where Q is the radiant energy. The SI derived unit is the watt.

radiation **1** the emission of energy from a source and its transmission as particles, rays, or waves, especially as electromagnetic rays or waves, sound waves, or streams of subatomic particles. **2** energy so transmitted, especially the corpuscular and electromagnetic rays emitted in the decay of radionuclides. **3** **ionizing radiation**. **4** divergence from a common point, especially radially from a central point or source.

radiation absorbed dose *see* **absorbed dose**, **rad** (def. 2).

radiation biology *an alternative name for* **radiobiology**.

radiation-chemical reaction any chemical reaction that is initiated by the absorption of radiation but is distinguishable from a **photochemical reaction** by its lack of specificity (i.e. by

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giving rise to a variety of reaction products) and by occurring at higher radiation energies (i.e. by absorption either of electromagnetic radiation from the mid-ultraviolet region onwards or of high-energy particulate radiation) and thus by resulting always in the formation of detectable ions.

radiation chemistry the branch of chemistry concerned with **radiation-chemical reactions**. *Compare* **radiochemistry**.

radiation damage the totality of the harmful changes induced in a cell or tissue by radiation. The harmful effects may include formation of **thymine dimers** in DNA or of radicals from polyunsaturated acyl groups in lipids.

radiation dose equivalent *see* **dose equivalent**.

radiation inactivation method a technique, based on **target theory**, that enables the size of the functional unit of a biologically active macromolecule (or of its complexes with other molecules) to be estimated; it can be used on unpurified (e.g. membrane-bound) material. Determinations are made of the biological activity remaining in a sample after exposure to various large doses of ionizing radiation (electrons or X- or gamma radiation of at least 1 MeV), and the value, D_{37}, of the radiation dose, expressed in Mrad, required to reduce the activity to 37% of (i.e. e^{-1} times) its original value is obtained; the relative molecular mass, M_r, of such a macromolecule may then be found from the empirical relationship

$M_r = 6.4 \times 10^5/D_{37}$, where D_{37} is determined at 30 °C.

radiation source a quantity of radioactive material used as a source of ionizing radiation.

radical *(in chemistry)* **1** any molecular entity, charged or uncharged, that possesses an unpaired electron (but normally excluding any paramagnetic metal ion); often formed by homolysis of a covalent bond. Radical character is indicated in a formula by a centred dot symbolizing the unpaired electron and placed (if possible) beside the symbol for the atom of highest spin density; e.g. HOO·, $\cdot CH_3$. The term **free radical** is now preferably restricted to any radical that does not form part of a **radical pair**. **2** *a former name for* **group** (def. 2).

radical anion *see* **radical ion**.

radical cation *see* **radical ion**.

radical centre the atom in any polyatomic **radical** (def. 1) on which the unpaired electron is largely localized.

radical ion any **radical** (def. 1) that carries an electric charge. One carrying a negative charge is termed a **radical anion** (e.g. the benzene radical anion, $C_6H_6^{\cdot -}$); one carrying a positive charge is termed a **radical cation** (e.g. the benzene radical cation, $C_6H_6^{\cdot +}$).

radical pair any two **radicals** (def. 1) in close proximity in liquid solution, with a solvent cage. They may have been formed simultaneously, e.g. by homolysis, or have come together by diffusion. Whilst together, correlation of their unpaired electron spins occurs and manifests itself as a distortion of nuclear magnetic resonance spectra.

radical scavenger any substance that can react readily with, and thereby eliminate, radicals. In biological systems or materials, radical scavengers may function as **antioxidants** or may protect from damage by ionizing radiation. Among the important radical scavengers that function in animal tissues at physiological concentrations are the water-soluble substances ascorbate, glutathione, and the purine bases, and the fat-soluble substances tocopherols, the retinols, the carotenes, and the ubiquinones.

radioactivate to convert a stable nucleus into one undergoing radioactive decay by bombardment with high speed particles, including protons, alpha particles, neutrons, and deuterons. These are formed in a cyclotron or synchrotron from a radioactive source, and accelerated through a potential difference of a few thousand volts by a magnetic field before being focused on the substance to be converted.

radioactivation analysis *or* **activation analysis** a method for the qualitative and/or quantitative estimation of the chemical elements in a sample. It depends on the identification and determination of the radionuclides formed when the sample is bombarded with neutrons or other particles.

radioactive having the properties associated with a **radioactive isotope**.

radioactive concentration the **activity** (def. 2) per unit quantity of any material in which a **radionuclide** occurs. *See also* **specific activity**.

radioactive decay *see* **decay** (def. 1b).

radioactive isotope *or* **radioisotope** any isotope of a chemical element whose nucleus is unstable and emits alpha, beta, or gamma rays. The product is another element, which may be stable or unstable; if the latter, it decays further. Thus, the principal isotope of uranium, ^{238}U, emits an alpha particle and decays to ^{234}Th, which emits a beta particle forming ^{234}Pa; this chain continues to the formation of ^{206}Pb, which is stable.

radioactive label *or* **radiolabel** a **radioactive isotope** incorporated into a molecule to confer on it the property of radioactivity.

radioactive tracer *or* **radiotracer** a radioactive substance that is added to a metabolic system in quantities (mass) too small to perturb the system, in order to follow, by isolating the radioactive intermediates formed, the sequence of transformations undergone normally by the same (nonradioactive) molecule under similar conditions.

radioactivity **1** the emission of radiation from certain **nuclides** by the spontaneous transformation of their **nuclei**. **2** *(loosely)* the radioactive material itself or its emitted radiation. *See* **activity** (def. 2).

radioallergosorbent test *abbr.*: RAST; a test used primarily for quantifying the levels of antigen-specific immunoglobulin E (IgE) in serum. A specific allergen, which has been covalently coupled to an insoluble **Sephadex** carrier, is incubated with serum containing the unknown amount of IgE. The carriers are then washed and further incubated with radiolabelled antibodies to IgE, the amount of radioactivity bound being a measure of the amount of IgE. The advantage of this method over the **radioimmunosorbent test** is that IgE specific to a particular antigen can be selectively quantified.

radioassay any type of **assay** in which a radioactive isotope is used in the measurement. The term embraces, e.g., **immunoradiometric assay**, **radioimmunoassay**, and competitive protein-binding assay.

radioautogram *or* **radioautograph** *or* **autoradiogram** the pattern formed after development of an X-ray film that has been exposed to a paper, gel, or thin-layer chromatogram containing radioactive compounds.

radioautograph **1** *an alternative term for* **radioautogram**. **2** to prepare a radioautogram. —**radioautography** *n.*

radiobiology *or* **radiation biology** the study of the interaction between radiation and biological material.

radiocarbon any radioactive isotope of carbon, usually carbon-11 or carbon-14.

radiochemical purity *abbr.*: RCP; the proportion of the total **activity** (def. 2) that is present in the stated chemical form in a radioactive material.

radiochemistry the branch of chemistry concerned with the compounds of radioactive nuclides. *Compare* **radiation chemistry**.

radiochromatogram a chromatogram of substances some or all of which contain a radioactive isotope.

radiofrequency radiation electromagnetic radiation encompassing wavelengths in the region 1 mm (300 GHz) to 30 km (10 kHz) (frequencies in parentheses). This range includes microwave radiation and lies above that of infrared radiation.

radiography the use of X-rays to examine the internal structures of a body. An X-ray film is placed behind the body, through which X-rays are passed. After exposure, there are areas of the film in which development has not occurred due to absorption of the X-rays by structures of the body, thus yielding a pattern of these structures. —**radiographer** *n.*; **radiographic** *adj.*; **radiographically** *adv.*

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radioimmunoassay *abbr.*: RIA; a highly sensitive method of assay of nonradioactive material. A known amount of antibody (Ab) directed against the substance (antigen, Ag) to be assayed is saturated with a mixture of Ag and radioactive Ag (Ag*), so that total Ag (Ag + Ag*) is in excess. When nonradioactive Ag is added to Ab along with Ag*, Ag and Ag* compete for binding to Ab, so that less Ag* will be found in the antibody–antigen complex as the ratio Ag:Ag* increases. If the antibody–antigen complex is then separated from free antigen, the total amount of antigen (the substance being assayed) can be calculated from the ratio Ab-Ag*:Ag* and the known **titre** of antibody. It is often convenient to attach the antigen to plates so that the amount of ligand bound to the plate is proportional to the amount of test antibody.

radioimmunosorbent test *abbr.*: RIST; a test used primarily for quantifying total serum immunoglobulin E (IgE) levels. Antibodies specific for IgE, covalently linked to an insoluble dextran, are incubated first with a known amount of radiolabelled IgE and then with the serum containing the unknown amount of IgE. From the decrease in the amount of radiolabel bound to the immobilized antibodies, due to competition by the unlabelled IgE in the serum, the total amount of IgE in the serum can be estimated.

radioiodinate to incorporate one or more atoms of **radioiodine** (usually iodine-125 or iodine-131) into a molecule.

radioiodine any radioactive isotope of **iodine**, notably iodine-125 (half-life 60 days) and iodine-131 (half-life 8 days).

radioisotope a **radioactive isotope**.

radiolabel **1** a **radioactive label**. **2** to incorporate a radiolabel.

radioligand any **ligand** containing a radioactive isotope; *see also* **Scatchard plot**.

radiology the study and use of radiation and radioactive substances, especially in the diagnosis and treatment of disease. It includes the use of diagnostic X-rays in **radiography**, the therapeutic use of ionizing radiation to treat disease (**radiotherapy**), and the experimental and diagnostic use of radioisotopes introduced into the body. —**radiological** *adj.*; **radiologically** *adv.*; **radiologist** *n.*

radiolysis the cleavage of chemical bonds by high-energy radiation. —**radiolytic** *adj.*; **radiolyse** *vb.*

radiometer **1** any instrument used to measure radiant energy. **2 Crookes radiometer** a specific type of radiometer in which the different behaviour of a polished surface, which reflects energy, and a blackened surface, which absorbs it, is utilized to cause a rotor to turn at a rate related to the intensity of radiation. [After William Crookes (1832–1919), British chemist and physicist.] —**radiometric** *adj.*; **radiometry** *n.*

radiomimetic **1** describing any drug or other chemical substance, typically an alkylating agent, whose effects in living systems (e.g. carcinogenic, immunosuppressive, mutagenic) resemble those produced by **ionizing radiation**; more loosely, describing any such agent able to cause gene and chromosome mutations. **2** a radiomimetic (def. 1) substance or agent.

radionuclide a radioactive **nuclide**. —**radionuclidic** *adj.*

radionuclidic impurity any radionuclide, other than the nuclide that should be present, in a radioactive material.

radionuclidic purity *or* **radiopurity** (of a radioactive material) the proportion of the total **activity** (def. 2) that is in the form of the stated **radionuclide**.

radiotherapy *see* **radiology**.

radiotracer *an alternative name for* **radioactive tracer**.

radixin a protein of the erythrocyte band 4.1 family present in a variety of eukaryotic cells; it shares about 75% homology with human **ezrin**. It is an actin barbed-end capping protein, highly concentrated in the undercoat of the cell-to-cell **adherens junction** and the cleavage furrow in the interphase and mitotic phase. Example from human: database code RADI_HUMAN, 583 amino acids (68.49 kDa).

radyl *(in chemical nomenclature)* a term used to indicate any acyl, alkyl, or alkenyl group where this cannot be specified in detail.

RAF any of a family of genes encoding Raf proteins; there are at least three Raf proteins, Raf-1, A-Raf, and B-Raf. These are protooncogene cytoplasmic serine/threonine protein kinases (EC 2.7.1.–) of the Ras/Mos family; they show similarity to members of the protein kinase C family in both their conserved C-terminal catalytic and regulatory N-terminal domains. Example, Raf-1 (human), which has binding domains for ATP, phorbol ester, and diacyl glycerol: database code KRAF_HUMAN, 648 amino acids (72.97 kDa). This protein is involved in transduction of mitogenic signals from the cell membrane to the nucleus. In the mouse, *raf* is the transforming gene of the mouse sarcoma virus, 3611, v-Raf having a truncated regulatory domain that causes constitutive activation of kinase activity. The c-Raf-1 protein kinase, a 74 kDa protein, has been found in all mammalian cells tested. Raf-1 is an important mediator of signals involving cell growth, transformation, and differentiation and is activated by a wide variety of extracellular stimuli. It has **MAP kinase** kinase kinase activity. In many cell types, Raf functions immediately downstream of the G-protein Ras (*see* ***RAS***) in the activation pathway; although Ras does not directly activate Raf, it mediates translocation of Raf-1 from cytoplasm to plasma membrane where it is activated. In some cells Raf may be phosphorylated and activated by members of the protein kinase C family. The first physiological substrate to be discovered for Raf kinase was a protein kinase (MEK) of yeast that is required for meiotic recombination and which on phosphorylation can activate **MAP kinase**.

raffinose *or* **gossypose** *or* **melitose** *or* **melitriose** the **trisaccharide** *O*-α-D-galactopyranosyl-(1→6)-*O*-α-D-glucopyranosyl-(1→2)-β-D-fructofuranoside; it occurs in plants almost as commonly as sucrose, being present, e.g., in cereal grains, cotton seeds, and many legumes. It is the first member of a series in which galactosyl residues are attached to sucrose, others being the tetrasaccharide **stachyose** and the pentasaccharide **verbascose**; these are all synthesized from sucrose by transfer reactions in which an α-D-galactopyranoside of *myo*-inositol (i.e. galactinol) is the donor of the galactosyl residues.

r.a.m. *abbr. for* relative atomic mass.

Ramachandran plot *or* **conformational map** a plot that shows the ranges of bond angles that are permissible and the main types of structure of an L-polypeptide chain (e.g. α helix, β-pleated sheet). As the peptide bond, –C′O–NH–, is planar, a polypeptide chain has only two degrees of freedom per residue, the twist about the C^{α}–N bond axis, ϕ, and that about the C^{α}–C′ axis, ψ. Some foldings will be easily achieved; others will be impossible because they would bring neighbouring unbonded atoms or groups within van der Waals contact distances. The Ramachandran plot shows the permitted range within a plot of ϕ against ψ. [After G. N. Ramachandran (1922–).]

Raman, (Sir) Chandrasekhara Venkata (1888–1970), Indian physicist; Nobel Laureate in Physics (1930) 'for his work on the scattering of light and for the discovery of the effect named after him'.

Raman scattering the inelastic scattering of a photon by a molecule, producing in the scattered light weak radiation of frequencies not present in the incident light. The sample does not have an absorption band at the wavelength of the incident light (*compare* **fluorescence**) and the frequency differences between the weak Raman lines in the spectrum and the exciting line are characteristic of the scattering substance and independent of the frequency of the exciting line. [After C. V. **Raman**.]

Raman spectrum a plot of **Raman scattering** over a range of frequencies.

Ramón y Cajal, Santiago (1852–1934), Spanish anatomist and histologist; Nobel Laureate in Physiology or Medicine (1906) jointly with C. Golgi 'in recognition of their work on the structure of the nervous system'.

Ramsay, (Sir) William (1852–1916), British physical and inorganic chemist; Nobel Laureate in Chemistry (1904) 'in recog-

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nition of his services in the discovery of the inert gaseous elements in air, and his determination of their place in the periodic system'.

RAN a gene encoding a small nuclear G-protein, first identified as a well-conserved gene distantly related to *H-RAS*. Its product, Ran, interacts with **RCC1**, and the complex is involved in regulating cell-cycle progression and messenger RNA transport. In the absence of RCC1, GDP–Ran predominates and this results in activation of **M-phase-promoting factor** and chromatin condensation. The presence of RCC1 activates nucleotide exchange on Ran, increasing the amount of GTP–Ran and preventing premature chromatin condensation. Example from *Mus musculus*: database code RAN_MOUSE, 216 amino acids (24.42 kDa). *See also* **nuclear pore**.

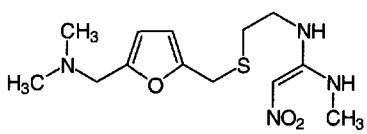
random coil the condition in solution of a linear polymer that exhibits little side group interaction, or resistance to rotation about the bonds in its chain. There are no preferred conformations. Quantitative expressions have been developed for the average radius of gyration. The term has formerly been incorrectly applied to various states of protein chains.

random copolymer a polymer of more than one species of monomer, in which the sequence of species within the polymer is not predetermined by controlled steps during synthesis, but depends only on random collisions between the reactant molecules. An example is the sequence of bases in RNA synthesized from nucleoside diphosphates by **polynucleotide phosphorylase**.

random mechanism *or* **random pathway** (for an enzymic reaction involving two substrates, A + B ⇌ C) a mechanism in which the enzyme, E, may first react with either substrate and the resulting enzyme–substrate complex then reacts with the second substrate, e.g. A + E ⇌ EA then EA + B ⇌ EAB, or, B + E ⇌ EB then EB + A ⇌ EAB, subsequently EAB ⇌ E + C. *Compare* **ordered mechanism**.

random sample a selection of part of a population made in such a way that no individual is favoured over any other individual. *See also* **sample, statistical sample**.

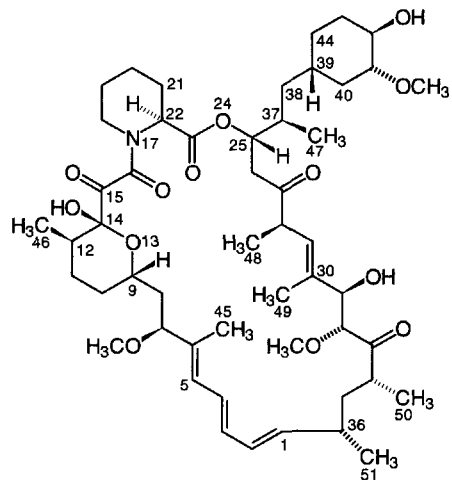
ranitidine a competitive antagonist at histamine H_2 receptors, being the major and pharmacologically more selective analogue of the imidazole derivative, **cimetidine**. It inhibits histamine- and pentagastrin-evoked gastric acid secretion and cardiac stimulation and also inhibits gastric secretion evoked by physiological stimuli, agonists at muscarinic cholinoceptors, and gastrin. It is used in the treatment of gastric and duodenal ulcers. *One proprietary name*: Zantac (hydrochloride).



RANTES *abbr. for* regulated upon activation, normal T-cell expressed and secreted chemokine; *other names*: small inducible cytokine A5; a chemokine secreted by T cells and macrophages on stimulation by mitogens, that acts as a chemoattractant, and stimulates basophils and eosinophils. Example from human (precursor): database code SISD_HUMAN, 91 amino acids (10.07 kDa); residues 1–23 are the signal, 24–91 RANTES.

ranunculeic acid *another name for* **columbinic acid**.

rapamycin an immunosuppressant (and antifungal agent) from *Streptomyces hygroscopicus*; it is used to reduce rejection of organ transplants. It is a lipid-soluble macrocyclic lactone, with the unusual feature of a cyclohexane ring with hydroxyl and methoxyl substituents. It competes with **FK506** for a common binding site on **FKBP**. *See also* **cyclosporin**.



rapamycin

RAPD PCR *abbr. for* random polymorphic DNA PCR; a variation of the **polymerase chain reaction** in which many short (≈10 nucleotide) primers are used. The products of the reaction from different sources can lead to recognition of polymorphisms and physical maps.

rape *or* **colza** a herbaceous plant, *Brassica napus*, of the mustard family, Cruciferae; it resembles a turnip, and the seeds yield valuable **rapeseed oil**.

rapeseed oil oil derived from the seed of **rape**; it is widely used as a lubricant and cooking fuel, and for the manufacture of animal foodstuffs, soap, and synthetic rubber. It contains **erucic acid**, which has cardiotoxic effects varying with species; rape varieties of low erucic acid content have recently been developed.

rapid-reaction kinetics the kinetic analysis of an enzyme reaction before the steady state is reached. The **stopped-flow method** is commonly used, in which two independent sources of substrate and enzyme are mixed immediately before flow through a spectrophotometer cell. An opposing syringe stops the flow immediately before activating the detection and recording system, such that reaction times of a few milliseconds can be achieved. Characteristically, reaction rates may be appreciably faster than during the steady state. In the **quenched flow** modification of the method, a further reagent is added to stop the reaction immediately before detection and recording. *See also* **relaxation kinetics**.

Rapoport–Lübering shunt a unique feature of erythrocyte glycolysis in which the glycolytic intermediate 3-phosphoglyceroyl phosphate is converted by bisphosphoglycerate mutase to 2,3-bisphosphoglycerate, which is in turn converted to 3-phosphoglycerate and inorganic phosphate by bisphosphoglycerate phosphatase, both reactions being catalysed by a single enzyme molecule. The shunt bypasses the near equilibrium phosphoglycerate kinase reaction, one of the two ATP-generating reactions of glycolysis. Since 2,3-bisphosphoglycerate is an important intracellular modulator of hemoglobin function, regulation of the Rapoport–Lübering shunt balances the energy needs and oxygen-transporting function of the red cell. [After Samuel Mitja Rapoport (1912–) and J. Lübering.]

rare earth *(strictly)* an oxide of a **rare earth metal**, *or (more loosely)*, a rare earth metal itself.

rare earth metal *or* **rare earth element** scandium, yttrium, or a **lanthanoid**.

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RAS an oncogene (v-*ras*) first discovered in the retroviruses Harvey and Kirsten rat sarcoma viruses; three closely related (85% homology) oncogenes are now known, Ha-*ras*, Ki-*ras*, and N-*ras*. Their cellular counterparts encode 21 kDa guanine nucleotide-binding proteins that play a pivotal role in regulating growth and differentiation in nearly every eukaryotic cell studied. There are two subfamilies, the Rho and Rac proteins (involved in relaying signals from the cell-surface receptors to the actin cytoskeleton) and the Rab family (involved in regulating the traffic of intracellular transport vesicles). Ras proteins undergo a number of modifications of the N and C termini that result in their localization to the plasma membrane. Ras binds both GTP and GDP with high affinity. It is considered active in the GTP-bound form and inactive in the GDP-bound form. The intrinsic rate of nucleotide exchange and GTPase activity is very slow. Ras·GDP predominates in resting cells, but when Ras is activated by occupied receptors, specific guanine nucleotide exchange factors (GEFs), e.g. **Sos**, enhance nucleotide exchange leading to Ras·GTP, GTP exceeding GDP in cytoplasm. Ras·GTP then activates downstream effector proteins such as Raf-1 (*see* ***RAF***). Activated GTPase activating protein (GAP) causes the formation of inactive Ras·GDP. The retroviral oncogene, v-*ras*, encodes a protein that differs from the c-*ras* product as a result of a point mutation. If this affects amino acids 12, 13, 59, 61, or 63 the protein fails to hydrolyse its bound GTP and so persists abnormally in its active state, constitutively transmitting an intracellular signal for cell proliferation. Alternatively, some transforming mutations increase the rate at which Ras can exchange guanine nucleotides, e.g. when amino acids 116, 117, 119, or 146 are affected, again increasing the amount of Ras·GTP. Activated *ras* oncogenes have been found in up to 30% of all human tumours analysed, with the most common point mutations being at codons for amino acids 12 and 13. In some types of malignancy, the figure is nearly 100%. Two genes corresponding to H-*ras* occur in yeast; they encode **G-proteins** that inhibit **adenylate cyclase**. 3-D structure known (including GDP bound to guanine nucleotide-binding domain) for human protein H-Ras-1: database code NRL_4Q21, 168 amino acids (19.07 kDa).

RAST *abbr. for* radioallergosorbent test.

rate coefficient *see* **rate constant**.

rate constant *or* **rate coefficient** *symbol*: k; a constant relating the concentration of a reactive species to the velocity of a reaction; thus for a first order reaction (*see* **order of reaction**) such as: EA → E + A, the rate of reaction, v, is proportional to the concentration of the reactant EA, so $v = k[EA]$, where k is the first-order rate constant. For a second order reaction, e.g. E + A → EA, the rate is proportional to the product of the reactant concentrations, i.e. $v = k[E][A]$, where k is the **second-order rate constant**.

rate-determining step *see* **rate-limiting step**.

rate-limiting step the slowest step in a reaction sequence; i.e. the step with the smallest rate constant.

rate of consumption *see* **rate of reaction**.

rate of conversion *symbol*: $\dot{\xi}$; for a specified chemical reaction, the rate of increase of the extent of reaction at any moment in time, regardless of the conditions under which the reaction is carried out: $\dot{\xi} = d\xi/dt$, where ξ is the extent of reaction and t is time. In the case of a reaction with one-to-one stoichiometry, such as a typical simple enzyme-catalysed reaction, the extent of reaction is equal to the amount of a reactant consumed or the amount of a product formed. Rate of conversion is an extensive quantity (*see* **extensive property**), its dimensions are (amount of substance) divided by time, and it is expressed in mol s^{-1} (*compare* **rate of reaction**). It is therefore independent of the volume of the system. Where this volume remains constant, as during a typical enzyme-catalysed reaction, the rate of conversion is equal to the rate of reaction multiplied by the volume: $\dot{\xi} = vV$. The term was formerly known in physical chemistry as rate of reaction. *See also* **catalytic activity**.

rate of formation *see* **rate of reaction**.

rate of reaction *or* **velocity of reaction** *or (sometimes)* **reaction rate** **1** *symbol*: v; for a specified enzyme-catalysed reaction of a typical kind (i.e. one involving a single substrate, S, a single product, P, one-to-one stoichiometry between them, and constant-volume conditions), the **rate of consumption** of substrate or the **rate of formation** of product at any moment in time is given by:

$$v = -d[S]/dt = d[P]/dt,$$

where [S] and [P] are respectively the concentrations of substrate and product, and t is time. A similar set of relationships applies where there are several reactants in one-to-one stoichiometry, but if the overall stoichiometry is not one-to-one – a situation rarely arising in enzyme kinetics – the relationships are more complicated. Where intermediates are formed in amounts comparable to those of the reactants, there is time-dependent stoichiometry and a rate of reaction for the complete reaction cannot be specified. Rate of reaction is an intensive quantity (*see* **intensive property**), its dimensions are (amount-of-substance concentration) divided by time, and it is expressed in mol L^{-1} s^{-1} (*compare* **rate of conversion**). *See also* **initial velocity**, **limiting rate**. **2** *(formerly, in physical chemistry)* the extensive quantity now termed **rate of conversion**.

rate theory of agonist action a theory of agonist action stating that the response to an agonist is proportional to the number of receptor–agonist associations per unit time, i.e. to the rate of receptor occupation, the binding of agonist to receptor being reversible. The response is therefore maximal at time zero and falls exponentially to an equilibrium value.

Rayleigh *see* **Strutt**.

Rayleigh ratio *symbol*: R; the ratio of the intensity of light scattered by particles (molecules) in solution at an angle θ from the incident beam, I_θ, multiplied by the square of the distance, r, from the particle to the detector, divided by the intensity of the incident light, I_o, i.e. $R = I_\theta r^2/I_o$. The **reduced Rayleigh ratio**, $R_\theta = I_\theta r^2/I_o(1 + \cos^2\theta)$. Many literature references do not distinguished between these two. *See also* **Rayleigh scattering**. [After J. W. **Strutt**, Lord Rayleigh.]

Rayleigh scattering the elastic scattering of photons of light by molecules or atoms of the substance through which the light is passing. When light passes through a liquid or gas, atoms or molecules are polarized by the electric vector of the light, thus inducing a rapidly fluctuating dipole in the atoms or molecules in the light path. The fluctuating dipole leads to the emission of electromagnetic waves in various directions of the same frequency as the incident radiation, and this emission is seen as scattered light. *See also* **Rayleigh ratio**. [After J. W. **Strutt**, Lord Rayleigh.]

Rb *symbol for* rubidium.

RB a human **tumour suppressor gene** that encodes a nuclear phosphoprotein, **retinoblastoma protein**. Inactivation or loss of *RB* on both copies of the chromosome (13q14) leads to **retinoblastoma**.

R band *see* **Giemsa's stain**.

RBC *or* **rbc** *or* **r.b.c.** *abbr. for* red blood cell. *See* **erythrocyte**.

Rbe *abbr. for* relative biological effectiveness (i.e. **quality factor**).

RBS *abbr. for* Réné Borghgraef solution; *the proprietary name for* any of a range of general-purpose surfactants and decontaminating agents, especially for laboratory use, that have combined detergent and chelating properties. They are identified with a number or other designation, e.g. RBS 25, RBS 35, RBS solid.

RCC1 a chromatin-bound guanine nucleotide release (or exchanging) factor. Its function is required for the normal coupling of the completion of DNA synthesis and the initiation of mitosis, and in its absence mitosis initiates before DNA replication is complete. RCC1 therefore appears to be involved in the regulation of this process. It is also necessary for RNA export from the nucleus. It binds to and acts on the nuclear G-protein, **Ran**. Example from the yeast *Candida albicans*:

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database code RCC_CANAL, 464 amino acids (51.27 kDa). [From regulator of chromosome condensation.]

RCF *abbr. for* relative centrifugal force.

R chromophore a **chromophore** that gives rise to low-intensity absorption bands at long wavelengths. *Compare* **K chromophore**. [From German *Radikal*.]

RCP *abbr. for* radiochemical purity.

RCS *abbr. for* rabbit aorta-contracting substance.

rd *symbol for* rad (def. 2) (alternative to rad).

Rd *abbr. for* rubredoxin.

rDNA **1** *abbr. for* ribosomal DNA. **2** *(sometimes) abbr. for* recombinant DNA; use not recommended because of possible confusion with ribosomal DNA.

Re- *prefix (in chemical nomenclature)* denoting *rectus* (i.e. right, or clockwise) configuration of a face of a trigonal atom. *See* ***Re/Si* convention**.

Re *symbol for* rhenium.

Re *symbol for* Reynolds number.

RE *abbr. for* (eukaryotic) response element.

reactancy of enzymes the number of reactants involved in an enzyme-catalysed reaction in a given direction. The numbers of kinetically important substrates or products in an enzyme mechanism are designated by Uni (1), Bi (2), Ter (3), or Quad (4). Thus, e.g., Uni Uni indicates one substrate and one product, and Ter Bi indicates three substrates and two products.

reactant any material participating in a chemical reaction in a given direction.

reaction *(in chemistry)* any process in which molecules interact with one another, leading to chemical or physical change.

reaction centre *see* **photosystem**. *Compare* **photosynthetic reaction centre**.

reaction intermediate a transient chemical species, with a lifetime appreciably longer than a molecular vibration time, formed directly or indirectly from the reactants of a chemical (often enzymic) reaction, and that further reacts (directly or indirectly) to give the reaction products.

reaction rate *(sometimes) an alternative term for* **rate of reaction**.

reaction time *an alternative name for* **latent period** (def. 1).

reactivate to restore activity to any enzymic or cellular system.

reactive describing any molecular entity or centre that is capable of reacting readily. Thus, a **reactive centre** is the point in the molecule at which electron configurations favour a reaction.

reactive oxygen a highly active oxygen species, such as **superoxide** ion.

reactivity the degree to which a molecule or centre is reactive.

reading *(in molecular biology)* the process of one-way linear decoding of a nucleotide sequence during, e.g., **transcription** or **translation**.

reading frame any sequence of bases in DNA that codes for the synthesis of either a protein or a component polypeptide. The point of initiation of reading determines the frame, i.e. the way in which the bases will be grouped in triplets as required by the genetic code. For example, the sequence

–ATGGTCA–

could be grouped

–A,TGG,TCA–

or

–AT,GGT,CA–

or

–ATG,GTC,A–

depending on the point at which the reading frame begins. *See also* **open reading frame**.

readthrough the continuation of DNA transcription beyond a normal termination sequence, due to a failure of RNA polymerase to recognize the termination signal. Readthrough may also occur in translation, where a mutation has caused a termination codon to be converted to a codon for an amino acid (a sense codon); this is the underlying etiology of several **hemoglobinopathies**. *See also* **readthrough protein**.

readthrough protein a product formed by translation of a messenger RNA when one of its termination codons is misread or is recognized by a **suppressor tRNA**. Polypeptide-chain synthesis then continues until the next termination codon is reached, resulting in the production of a variant protein with a C-terminal extension.

reagent **1** any chemical substance that reacts or participates in or is necessary for a reaction. **2** a substance used for the detection or determination of another substance by chemical or microscopical means, usually in solution; e.g. the **Folin–Ciocalteu reagent**.

reagent grade a level of purity of a chemical; chemicals of this quality conform to the specifications established by the Committee on Analytical Reagents of the American Chemical Society and may often be sufficiently pure to use as primary standards in an analytical laboratory, with information concerning the actual percentage of impurities or at least the maximum limit of impurities being given on the label.

reagin **1** *a term originally used to describe* a heat-labile antibody-like substance in the serum of many people suffering from atopic allergies and that has now been identified as immunoglobulin E (IgE). The **immediate hypersensitivity** (type I) generated by the binding of IgE to its specific antigen on the surface of mast cells involves the release of cell mediators via the reaginic or anaphylactic mechanism. **2** a special kind of antibody response produced by syphilitics that has specificity for **cardiolipin** antigens.

real-time *(in computing)* indicating that a computer monitors a process continuously as it occurs, in distinction to the analysis of recorded data.

rearrangase *or* **S–S rearrangase** *an alternative name for* **protein disulfide isomerase**.

rearrangement reaction a reaction in which molecular bonds are rearranged without the loss of any atom from the molecule, e.g. as in the conversion of glucose 6-phosphate to fructose 6-phosphate.

recA a gene in *Escherichia coli* encoding a protein, RecA, involved in **genetic recombination** and in the SOS response for DNA repair (*see* **SOS repair**). The protein has two activities: (1) a DNA-dependent ATPase in the presence of single-stranded DNA that catalyses the ATP-dependent uptake of single-stranded DNA to form the heteroduplex required in recombination. (2) In the presence of DNA fragments it becomes a protease (RecA*; EC 3.4.99.37) that cleaves a specific Ala-|-Gly bond in certain repressor molecules, including its own repressor (*see* ***lexA***). This allows all the SOS genes to be activated. Example from *E. coli* and *Shigella flexneri* (identical sequences): database code RECA_ECOLI, 352 amino acids (37.80 kDa); 3-D structure known; eight motifs. *See also* **exodeoxyribonuclease V**, **recombinational repair**, **recombinase**.

recalcitrance *or* **persistence** the ability of a substance to remain in a particular environment in an unchanged form.

recBC a gene in *Escherichia coli* for **exodeoxynuclease V**, an ATP-dependent nuclease specific for double-stranded DNA; it mediates **genetic recombination**.

recDNA *(sometimes) abbr. for* recombinant DNA.

receptor any cellular macromolecule that undergoes combination with a hormone, neurotransmitter, drug, or intracellular messenger to initiate a change in cell function. Receptors are concerned directly and specifically in chemical signalling between and within cells. Cell-surface receptors, e.g. the **acetylcholine receptor** and the **insulin receptor**, are located in the plasma membrane, with their ligand-binding site exposed to the external medium. Intracellular receptors, e.g. steroid-hormone receptors, bind ligands that enter the cell across the plasma membrane.

receptor assay **1** the determination of receptor numbers and the dissociation constant of receptor–ligand binding. The

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binding at various concentrations of ligand is measured, often by use of a radioactive ligand, and is analysed by means of a **Scatchard plot**. **2** the determination of the concentration of a ligand by utilizing a purified receptor in a manner similar to that used in **radioimmunoassay**; in this case the receptor, rather than an antibody, performs the role of specific binding agent.

receptor cross-talk interaction between two receptors such that one receptor, when activated, modulates the action of the other. This type of interaction often involves the production by the first receptor of a **second messenger**, which then modulates the action of the second receptor.

receptor-destroying enzyme an enzyme that brings about chemical change in a (usually membrane-bound) receptor, leading to inactivation of the receptor. Knowledge of the specificity of the enzyme provides information about the nature of the groups or linkages exposed to enzyme attack, and thus to receptor structure or orientation in the membrane. Examples are **sialidase** and **trypsin**.

receptor–effector complex the complex that results when an occupied receptor binds to another protein (the **effector**), the activation of which by the occupied receptor leads to signal transduction.

receptor-mediated describing a response that requires the intermediary action of a receptor, especially one located in a membrane.

receptor-mediated endocytosis a form of **endocytosis** involving the internalization (i.e. passage into the cell interior) of stretches of membrane into which receptors have clustered after binding of ligand. The cytoplasmic surfaces of these stretches of membrane are coated with **clathrin** and are termed **coated pits**. *See also* **endosome**.

receptor transformation *see* **transformation** (def. 3).

recessive describing an **allele** that lacks effect when accompanied in the same diploid by a **dominant** form of the same gene. Most (not all) defective mutant genes are recessive to their normal functional counterparts. —**recessivity** *n.*

recipient bacterium *see* **bacterial conjugation**.

reciprocal **1** expressed in the reverse direction, in response to an initial application of any force or stimulus. **2** *(in mathematics)* the inverse value, obtained when the values of numerator and denominator are reversed; the reciprocal of x is obtained by evaluating $1/x$.

reciprocal plot a plot in which the units of both the ordinate and the abscissa are reciprocals of the values that have been determined. *Compare* **Lineweaver–Burk plot**.

recircularization *or* **recircularisation** the restoration of circularity to a plasmid vector following the insertion of recombinant DNA. The plasmid used for gene cloning is a small circular molecule. This is cut with a **restriction endonuclease** to create linear DNA molecules. The foreign DNA fragment with the same cohesive ends is then annealed to the cut plasmid to form a recombinant DNA circle. The DNA molecule containing the foreign DNA insert is then covalently sealed with **DNA ligase**. Recircularization also occurs during the replication of some DNA phages by a **rolling circle** replication mechanism.

recognition any specific binding interaction between molecules. Such interaction between two molecules is based on the existence of **recognition sites**, one (or more) on each of the interacting molecules, that are tailored to fit in such a way that highly specific binding occurs; i.e. the two molecules uniquely 'recognize' each other. *See also* **chiral recognition**, **molecular recognition**.

recognition sequence the part of the sequence of a macromolecule that is able to recognize and bind to a particular sequence in another macromolecule.

recognition site **1** *(in proteins)* a site for **recognition** of another protein, involving a specific sequence of amino acids; the latter may be in a single chain (e.g. target sites for protein phosphorylation), or may involve amino acids in separate chains brought into juxtaposition by quaternary structure. **2** *(in nucleic acids)* a site for recognition of a protein, involving a specific sequences of bases; *see* **restriction endonuclease**. **3** *(in pharmacology)* a region of a receptor macromolecule to which an endogenous agonist binds.

recombinant clone a population of bacteria or other host derived from a single cell into which a vector containing **recombinant DNA** has been introduced.

recombinant DNA a fragment of deoxyribonucleic acid (DNA) that has been inserted into a cloning vector, thereby leading to its use in the isolation of a clone of cells characterized by the presence of the fragment. The term is derived from the concept that insertion into the vector is a form of **genetic recombination**. [*Note*: The abbreviation rDNA has sometimes been applied to recombinant DNA, but this use is discouraged (rDNA having been pre-empted for ribosomal DNA); while alternatives such as recDNA or rtDNA have been suggested, IUBMB considers a standard abbreviation unnecessary.] *See also* **recombinant DNA technology**.

recombinant DNA technology an area of biotechnology concerned with the manipulation of **recombinant DNA**. It has many important applications, including (1) DNA sequencing, which may lead to the ability to predict the primary structure of a protein where this is the product of a cloned gene, (2) the synthesis of recombinant protein by a suitable expression system, and (3) the production of DNA **probes** (def. 3) for use in hybridization techniques. The technology has led, e.g., to the production of human insulin for the treatment of diabetics, human growth hormone for administration to children with growth defects, and a vaccine for hepatitis B. DNA probes are essential for the detection of aberrant genes which are the cause of numerous diseases and the technique has the potential for gene therapy. *See also* **genetic engineering**.

recombinant protein a protein coded for by a gene – **recombinant DNA** – that has been cloned in a system that supports expression of the gene and translation of messenger RNA (*see* **expression system**). Modification of the gene by recombinant DNA technology can lead to expression of a mutant protein. Proteins coexpressed in bacteria will not possess post-translational modification, e.g. phosphorylation or glycosylation. Eukaryotic expression systems are needed for this; see, e.g., **baculovirus**.

recombinase **1** an enzyme that recognizes specific sites involved in the joining of V-region gene segments in L- and H-chain gene segment pools in the generation of antibody. **2** RecA protein (*see* ***recA***) is also a recombinase, the activity of which is increased in *Escherichia coli* following damage to DNA. RecA binds to a region of single-stranded DNA and catalyses the formation of duplex DNA; hydrolysis of ATP is involved. A recombinase recognizes and binds to each of two recombinant sites on different DNA molecules or within the same DNA. One DNA strand in each site is cleaved at a specific point within the site, and the recombinase becomes covalently linked to the DNA at the cleavage site through a phosphotyrosine (sometimes a phosphoserine) bond. The transient protein–DNA linkage preserves the phosphodiester bond lost in cleaving the DNA; cofactors such as ATP are unnecessary in subsequent steps. The cleaved DNA strands are rejoined to new partners, with new phosphodiester bonds created at the expense of the protein–DNA linkage. The result of the initial breakage and rejoining process is the **Holliday junction**. To complete the reaction, the process must be repeated at a second point within each of the two recombination sites. In summary the recombinase can be viewed as a site-specific endonuclease and ligase in one package.

recombination *see* **genetic recombination**, **recombinant DNA**, **immunoglobulin synthesis**.

recombinational heteroduplex *see* **heteroduplex**.

recombinational repair a mechanism to restore the integrity of DNA when replication of DNA stops at a **thymine dimer** but resumes after the dimer is passed, creating a gap. The undamaged parental strand recombines into the gap, a process promoted by RecA protein (*see* ***recA***). The new gap in the parental

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strand is filled by the action of **DNA polymerase** and **DNA ligase**. The thymine dimer itself is not repaired in this process but time is allowed for the excision system to repair this damage later.

recoverin an **EF-hand** Ca^{2+}-binding protein, apparent molecular mass 26 kDa; *also known as* **cancer-associated retinopathy protein**. It selectively localizes to the retina and pineal gland and is implicated in the activation of retinal rod guanylate cyclase by rhodopsin, possibly being involved in the blocking of the phosphorylation of rhodopsin, by forming an inhibitory complex with rhodopsin kinase. It has been identified as an autoantigen in cancer-associated retinopathy, a putative autoimmune process. Example from human: database code RECO_HUMAN, 199 amino acids (22.97 kDa).

recovery the portion of material or activity that remains after any extraction or purification, usually expressed as a percentage of the amount that was present as starting material.

recruitment the action by any cell, cell constituent, or molecule that brings about the cooperation of any other component in performance of any function.

recrystallize *or* **recrystallise** to dissolve a crystalline substance and subsequently crystallize it from the solution, usually to increase the purity of the substance. —**recrystallization** *or* **recrystallisation** *n.*

rectangular hyperbola a **hyperbola** whose asymptotes are at right angles. It is sometimes said that, for enzymes that follow so-called **Michaelis kinetics**, the plot of initial rate against substrate concentration has the shape of the curve of a rectangular hyperbola. It is true that the Michaelis–Menten equation does yield a curve that is part of a rectangular hyperbola, but the axes of the hyperbola must be rotated through 45°, and displaced, if they are to coincide with the axes of the Michaelis–Menten plot.

rectification **1** *(in physics)* the process of obtaining a direct current from an alternating electrical supply. **2** *(in physiology)* the regulation of membrane conductance by the voltage across the membrane; strong rectification implies that ionic channels carrying current are open at some membrane potentials and shut at others. Conductance is low at very negative membrane potentials, but increases as the potential becomes less negative. **3** *(in chemistry)* the process of purifying a liquid by distillation.

rectus *Latin* right; used to describe the right, or clockwise, configuration of one of the two faces of a compound containing a trigonal carbon atom. It is designated by the prefix *Re-*. *Compare* ***sinister***. *See also* ***Re/Si* convention**.

recycle to pass again through a system one or more times after return to a starting condition or state.

red drop a phenomenon in photosynthesis, in which the **quantum yield** is relatively constant in light of wavelengths between 500 and 600 nm, but drops dramatically at longer wavelengths.

redistil *or (US)* **redistill** to distil again that which has already been distilled, usually as an aid to purification of liquids.

red marrow *see* **bone marrow**.

red muscle dark, skeletal, voluntary muscle that is relatively rich in myoglobin and cytochromes, and derives energy for contraction from a high oxidative capacity, in contrast to **white muscle**, which has a high glycolytic capacity. The distinction between muscle types should more strictly be based on muscle-fibre types. Type I fibres have a high oxidative capacity based on a high activity of tricarboxylic-acid cycle and respiratory chain enzymes. Type IIA fibres have high oxidative and high glycolytic capacity. Type IIB fibres have low oxidative and high glycolytic capacity. The proportions of these fibres vary in different muscle types; accordingly the muscle may have the ability to engage in very rapid but quickly exhausted 'fast twitch' contractions characteristic of white muscle, or less powerful but more sustained contractions typical of red muscle.

redox *abbr. for* reduction–oxidation; *see* **oxidation–reduction**.

redox balance the ratio of the number of reductions to the number of oxidations in a given metabolic pathway. *Compare* **redox state**.

redox couple the oxidized (electron acceptor) and the reduced (electron donor) forms of the species of a given **redox reaction**; e.g. NAD^+ and ($NADH + H^+$). The potential of any redox couple in solution can be measured against a reference electrode, and a table of relative potentials constructed. *See* **redox potential**.

redox hypothesis a now discounted model for the **Pasteur effect** in glycolysing muscle extracts. Addition of redox indicators that changed the redox state in the direction of oxidation decreased the rate of lactate formation; it was therefore suggested that the effect of oxygen might be connected with a change of the redox state in the same direction.

redox indicator *see* **indicator** (def. 3).

redox potential *or* **oxidation–reduction potential** *symbol*: E_o; for a particular **redox couple** at a given pH and temperature, the potential of an electrode (usually bright platinum) immersed in a solution containing 1 M oxidant and 1 M reductant, relative to a standard **hydrogen electrode**. The more 'reducing' the couple, the more negative is E_o; the convention in biochemistry is that the more 'oxidizing', the more positive is E_o. Some standard potentials, measured against the hydrogen electrode, are: $NAD^+/NADH + H^+$, –0.32 V; fumarate/succinate, +0.032 V; cytochrome $b(Fe^{3+})$/cytochrome $b(Fe^{2+})$, +0.22 V; cytochrome $c(Fe^{3+})$/cytochrome $c(Fe^{2+})$, +0.25 V; $O_2 + 2H^+/H_2$, +0.82 V.

redox reaction a chemical reaction in which the oxidation of one reactant is coupled to the reduction of a second reactant, electrons being transferred from the reactant being oxidized to that being reduced.

redox state the ratio of the concentration of the oxidized member of a **redox couple** to the concentration of the reduced member; e.g. $[NAD^+]/[NADH]$ or $[Fe^{3+}]/[Fe^{2+}]$. The term should only be applied to a particular redox system and not to a heterogeneous system.

red shift any shift of the peaks of a spectrum to longer wavelengths (i.e. towards the red end of the spectrum), including a shift from the red to infrared. *Compare* **blue shift**.

red tide a bloom of the dinoflagellate *Ptychodicus brevis* (*Gymnopodium breve*), an organism that produces **brevetoxins** and causes epidemics of food poisoning.

reduce to cause or undergo **reduction**.

reduced Rayleigh ratio *see* **Rayleigh ratio**.

reducing agent any substance acting as a **reductant**. *Compare* **oxidizing agent**.

reducing end the end of an oligo- or polysaccharide molecule that carries a potential hemiacetal or hemiketal (reducing) group.

reducing sugar any **sugar** that will reduce heated alkaline solutions of cupric salts, such as **Fehling's** or **Benedict's solutions**, due to the presence of a hemiacetal or hemiketal group.

reductant the chemical species that donates an electron in an **oxidation–reduction reaction**; i.e. the species that undergoes **oxidation** in such a reaction. *Compare* **oxidant**.

reductase a donor:acceptor oxidoreductase enzyme (EC class 1) when named after the more oxidized alternative substrate and when O_2 is not a substrate. *See* **oxidoreductase**.

reduction the chemical process by which oxygen is withdrawn from, hydrogen is added to, or (more generally) an electron is added to (with or without addition of a proton) a molecular entity. *Compare* **oxidation**. —**reductive** *adj.*; **reduce** *vb.*

reduction division the first division of **meiosis**.

reduction potential the electrode potential that measures the tendency of one half of a **redox reaction** to proceed so as to gain electrons. *See* **oxidation potential**, **redox potential**.

reductive alkylation the reaction of amino groups with an alkyl carbonyl group, followed by reduction of the resulting **Schiff base** with a reducing agent such as sodium borohydride. *See* **reductive amination**.

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reductive amination the process whereby ammonia or a primary or secondary amine reacts with ketones and aldehydes in the presence of reducing agents such as H_2 and a metal catalyst, or more conveniently, $NaBH_4$ or its derivative $NaBH_3CN$, to produce primary, secondary, or tertiary amines. In a formal sense, the amine is alkylated in this reaction while the carbonyl group is reduced, hence the term reductive amination, or alternatively **reductive alkylation**. Amino acids have been made from oxo acids by this process. A variation of reductive amination, termed the **Eschweiler–Clarke reaction**, involves the methylation of an amine to the tertiary amine stage using formic acid as the reducing agent and formaldehyde as the methylating reagent.

reductive carboxylic-acid cycle *or* **reductive tricarboxylic-acid cycle** a metabolic cycle used by members of the Chlorobiaceae for CO_2 fixation. The usual operation of the tricarboxylic-acid cycle is reversed, with three enzyme replacements, and other supplementary reactions are used. Initially one CO_2 reacts with succinyl-CoA to form oxoglutarate; oxoglutarate synthase (EC 1.2.7.3) replaces the usual **oxoglutarate dehydrogenase complex**. A second CO_2 converts oxoglutarate to isocitrate with use of **isocitrate dehydrogenase**, and isocitrate proceeds to citrate. Citrate is then cleaved by ATP citrate *(pro-S)* lyase to acetyl-CoA and oxaloacetate; the latter recycles to succinyl-CoA with fumarate reductase (NADH) replacing succinate dehydrogenase. These operations reverse the usual tricarboxylic-acid cycle and convert two CO_2 to acetyl-CoA. A net gain of oxaloacetate is possible by conversion of acetyl CoA and one CO_2 to pyruvate (pyruvate synthase), pyruvate to phospho*enol*pyruvate (phospho*enol*pyruvate synthase) and **phospho*enol*pyruvate** and one CO_2 to oxaloacetate (**phospho*enol*pyruvate carboxylase**). The overall result is that four CO_2 yield a net gain of the four-carbon oxaloacetate.

reductive methylation a specific form of **reductive alkylation**, in which the alkyl group is methyl. Formaldehyde is often used as a reagent in this case.

reductive pentose-phosphate cycle *or* **Calvin cycle** *other names:* carbon reduction cycle; C_3 cycle/pathway; more appropriately, Calvin–Bassham cycle; the cyclic set of reactions, occurring in chloroplasts in the majority of higher plants (**C_3 plants**), that results in the fixation of CO_2 as glucose using the ATP and the NADPH formed in the light reactions of photosynthesis. Briefly, CO_2 reacts with ribulose 1,5-bisphosphate under the action of **ribulose-bisphosphate carboxylase** (Rubisco), EC 4.1.1.39, to form two molecules of 3-phosphoglycerate; these are phosphorylated (by ATP) to 1,3-bisphosphoglycerate, which in turn is reduced (by NADPH) to glyceraldehyde 3-phosphate. This is then converted by aldolase, transketolase, and other enzymes to fructose 6-phosphate and ribulose 5-phosphate; the latter being phosphorylated (ATP) to ribulose 1,5-biphosphate, completing the cycle. *See also* **Hatch–Slack pathway**.

reductone any reducing substance with a chemical structure containing the stabilized enediol –C(OH)=C(OH)–. Reductones are generated when monosaccharides are heated for prolonged periods with strong alkali, whereby the enols originally produced are broken down to strongly reducing fragments. Another notable example is ascorbic acid, and in some contexts reductones are described as '**apparent ascorbate**', i.e. the reductive acids that are present in certain processed foods and react similarly to ascorbate, interfering with its determination.

Re-face (of an atom or molecule) *see* ***Re/Si* convention**.

reference something that acts as a standard in relation to quality, quantity, or type against which other values or characteristics can be compared; e.g. reference spectrum.

reference electrode any electrode, selected by convention, against which the electronegativity of compounds is measured. The standard biochemical reference is the **hydrogen electrode**, normally a platinum electrode in hydrochloric acid through which hydrogen gas is passed. A cell is constructed such that another electrode is immersed in a test solution and the potential difference between these two half-cells is measured. For convenience, however, the reference electrode is often a **calomel electrode**, and after measurements have been made against this, the electronegativity against the hydrogen electrode can be calculated from the known difference between this and the hydrogen electrode.

reflect to change the path of electromagnetic radiation, when it meets a surface, such that it returns partially or completely in a direction on the same side of the surface as the source.

reflectometer *see* **densitometer** (def. 1).

reflex *(in physiology)* an automatic or involuntary response of the nervous system to a stimulus. A reflex may be a monosynaptic spinal reflex (e.g. a simple motor response to a sensory stimulus), involving transmission through the spinal cord only, or polysynaptic and involving synaptic transmission in the brain. A **conditioned reflex** is one that is learned through repeated association of a stimulus with either rewarding (e.g. food) or aversive (e.g. punishment) events.

refolding (for proteins) the restoration of three-dimensional structure in a manner that may or may not achieve a full return to the native state following **denaturation**.

refraction the change in direction undergone by a wave of electromagnetic radiation on passing through a boundary between two media in which its velocity differs. **Snell's law** states that $n_1 \sin\theta_1 = n_2 \sin\theta_2$, where n_1 and n_2 are the **refractive indices** of the two media, and θ_1 and θ_2 are the angles between the radiation and the normal to the boundary in the corresponding media. [After Willebrord Snell (1591–1696), Dutch astronomer and mathematician.]

refractive index *abbr.*: RI; *symbol*: n; for a given medium, a measure of the degree of **refraction** induced by the medium when light or other electromagnetic radiation passes through it. The refractive index of a medium is the ratio of the speed of light in a vacuum, c_0, to the speed of light in the medium, c; i.e. $n = c_0/c$. For many practical purposes the speed of light in air may be used instead of that in a vacuum.

refractivity a measure of the extent to which a medium will cause the deviation of a ray of light or other electromagnetic radiation entering its surface. If the **refractive index** of a medium is n, its refractivity is $(n - 1)$. The **specific refractivity** is given by $(n - 1)/\rho$, where ρ is the density of the medium. The **molecular refractivity** is the specific refractivity multiplied by the relative molecular mass.

refractometer an instrument for measuring **refractive index**.

refractory **1** (of a clinical condition) resistant to treatment. **2** (of a cell or tissue) resistant to stimulation, as by a drug, hormone, or nerve impulse, especially during a period following previous stimulation. *See also* **tachyphylaxis**. **3** (of a substance or material) resistant to heat, corrosion, mechanical deformation, or other aggressive agents causing alteration. **4** a substance or material having such resistance.

Refsum's disease a rare autosomal recessive inherited disease with neurological symptoms, including retinitis pigmentosa, peripheral neuropathy, cerebellar ataxia, and nerve deafness. It is caused by a defect in **alpha oxidation** of fatty acids, which is important for the oxidation of **phytanic acid**. The defect results in the accumulation of this acid in tissues and serum of patients. The symptoms are reduced by restriction of dietary dairy products and meat from ruminants, which contain phytanic acid.

regeneration **1** *(in chemistry)* the process of restoring to a state of preparedness for use, as in the case of an ion-exchange resin washed with acid or alkali to restore it to the H^+ or OH^- form. **2** *(in biology)* the growth of new tissues or organs to replace ones lost or damaged, e.g. through injury or surgery. In some tissues, such as liver, epithelial tissue, or pancreas, regeneration occurs by simple duplication of cells, with the **regeneration time** varying from one week to a year. In other systems, such as epidermis, renewal is from specialized **stem cells**. Regenerating liver can be used as a model in which systems involved in proliferation are more highly activated than

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in normal liver. It is a unique property of liver that it is possible to remove two thirds of the organ yet it regenerates to form an organ of similar total weight to the original, albeit with somewhat different organization of the lobes. Many plants can regenerate a complete plant from a shoot segment or a single leaf or from tissue culture cells.

regeneration time the time taken for a tissue or organ to regain its former size or weight following damage or removal. For example, if two-thirds of the liver of a rat is removed surgically the liver regains its former weight in about two weeks. The proliferation of cells can be measured by the use of [^{3}H]thymidine to label the cells synthesizing DNA.

regio+ *comb. form* denoting, or relating to, an area or site.

regioselective pertaining to a chemical change that occurs with greater frequency at one site than at a number of other possible sites of similar type, usually involving a structural or positional isomer.

regiospecific describing a chemical reaction that occurs specifically in only one of two possible ways, but not including stereospecificity (*see* **stereospecific**).

registration peptide one of the postulated extensions of the α chains of **tropocollagen**, when synthesis has just been completed; two α1 extensions and one α2 extension interact to form a stable assembly with the correct chains brought together into register.

regression coefficient *see* **regression line**.

regression line a line fitted to a series of two variable quantities, x and y, so as to minimize the sum of the squares of the distances parallel to the y axis of the observations from the line. The regression line of y on x has the equation (**regression equation**): $y = a + bx$ where $a = \Sigma y - b\Sigma x/n$ and b, the **regression coefficient**, is the slope of the line and is given by:

$$b = (n\Sigma xy - \Sigma x\Sigma y)/(n\Sigma x^2 - (\Sigma x)^2)$$

where n is the number of pairs of observations. In an analogous manner a regression equation, line, and coefficient may be obtained for x on y.

regucalcin a hepatic Ca^{2+}-binding protein, and also a GTP-binding protein, that modulates the hormonal regulation of plasma membrane Ca^{2+},Mg^{2+}-ATPase.

regulation *(in metabolism)* control of the rate of a metabolic system, especially in intact organs and cells as a result of interaction from components of related systems. —**regulatory** *adj.*

regulator gene *or* **regulatory gene** any gene that does not contribute structural information to the proteins whose synthesis it controls, but that determines the production of a specific cytoplasmic substance, a **repressor**, that inhibits information transfer from a **structural gene** (or genes) to protein. It may control the synthesis of several different proteins, which are determined by a coordinated group of structural genes (*see* **operon**). Although, when it was put forward, the concept of the regulatory gene was helpful, it is now realized that the genome codes for many different proteins that control the transcription of the structural genes (*see*, e.g., **attenuators**, **transcription factors**), and that can be classed as gene-activator proteins; these will possess two domains, one to recognize a specific regulatory DNA sequence, the other to contact the transcription machinery.

regulator-site hypothesis a hypothesis to explain the control of insulin release from pancreatic islet B cells by glucose. It postulates that the glucoreceptor is an enzyme that is activated (or inhibited) by glucose and catalyses the production from a precursor of an activator, which controls the release process. *Compare* **substrate-site hypothesis**.

regulatory enzyme an enzyme that regulates the rate of a metabolic pathway; under regulating conditions, it is the enzyme of lowest activity in the pathway. Commonly, the rate is altered either by variation in the amount of regulatory enzyme (as a result of increased or decreased synthesis or degradation), or by variation in its activity by covalent modification (often by phosphorylation or dephosphorylation by kinases or phosphatases) or by allosteric modifiers. Classic examples are **phosphofructokinase** and glycogen phosphorylase (*see* **phosphorylase**).

regulatory gene *see* **regulator gene**.

regulatory sequence a sequence in a DNA molecule concerned with regulating the expression of a gene; e.g. a **promoter** or **operator**.

regulatory site a specific site on an enzyme that is distinct from the substrate-binding site and that binds a feedback inhibitor or other regulatory molecule. *Compare* **allosteric site**.

regulatory subunit any of the subunits of a multimeric enzyme (composed of nonidentical subunits) that has a regulatory rather than a catalytic function.

regulon a group of genes, whether linked in clusters or unlinked, that respond to a common regulatory signal.

rehydrate to restore water to material that has been lyophilized (*see* **freeze-dry**) or otherwise dehydrated.

Reichstein, Tadeus (1897–1996), Polish-born Swiss chemical engineer, organic chemist, and botanist renowned for his isolation and study of 29 different steroids from the cortex of the adrenal gland and (in 1933) for devising a method of synthesizing ascorbic acid, vitamin C, from glucose that is still in use industrially; Nobel Laureate in Physiology or Medicine (1950) jointly with E. C. Kendall and P. S. Hench 'for their discoveries relating to the hormones of the adrenal cortex, their structure and biological effects'.

reiterated describing nucleotide sequences that occur many times within a genome. These occur especially in higher organisms. *See also* **repetitive sequences**.

REL a gene family encoding transcription factors of the κB family; v-*rel* is the oncogene of avian reticuloendothelial virus strain T (REV-T), encoding p69$^{v\text{-}rel}$. Rel and v-Rel form homo- or heterodimers that bind to **NF-κB** motifs. v-Rel has lost two N-terminal amino acids and 118 C-terminal residues compared with Rel. Example of Rel product from mouse: database code REL_MOUSE, 587 amino acids (64.96 kDa). Example of p69$^{v\text{-}rel}$: database code TREL_AVIRE, 503 amino acids (55.91 kDa).

relA a gene in *Escherichia coli*, mutations in which can lead to a 'relaxed' phenotype in which amino-acid starvation fails to switch off ribosomal RNA biosynthesis. The gene product is an enzyme active in the presence of ribosomes and uncharged tRNA, and called GTP pyrophosphokinase, EC 2.7.6.5; *systematic name*: ATP:GTP 3′-pyrophosphotransferase; *other names*: pppGpp synthetase I; **stringent factor**; guanosine 3′,5′-polyphosphate synthase; it catalyses a reaction between ATP and GTP to form guanosine 3′-diphosphate 5′-triphosphate and AMP. The product is referred to as pppGpp and is converted to ppGpp (guanosine 3′-diphosphate 5′-diphosphate), which is the active nucleotide in evoking the **stringent response**. Database code RELA_ECOLI, 744 amino acids (83.76 kDa).

relative atomic mass *or (formerly)* **atomic weight** *abbr.*: r.a.m.; *symbol*: A_r. **1** (of an atom) the ratio of the mass, m_a, of the atom in question, to the atomic mass constant, m_u, which is one-twelfth of the mass of the nuclide ^{12}C; i.e. $A_r = m_a/m_u$. A_r is a mass ratio, a pure number with no units. **2** (of an element) the ratio of the average mass, $\bar{m}_a$, of the atoms in a specified sample of the element in question, E, to the atomic mass constant, m_u; i.e. $A_r(E) = \bar{m}_a(E)/m_u$. Since, in general, elements are mixtures of isotopes of differing nucleon numbers (mass numbers), an average mass of the atoms is required in this definition. Furthermore, the isotopic composition of many elements can vary with the origin of the sample and its treatments. Hence there are limits to the precision with which the values of the relative atomic masses of many elements can be given.

relative band rate *or* **relative band speed** *see* ***R*$_B$ value**.

relative biological effectiveness *abbr.*: RBE; *an alternative term for* **quality factor**.

relative centrifugal force *symbol*: G; the force acting on a particle in a centrifugal field expressed in multiples of the ac-

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celeration due to gravity, g. $G = \omega^2 r$, where ω is the angular velocity in rad s^{-1} and r the radial distance from the axis of rotation in m. ($G = 1440 \times \pi^2\omega^2 r$ where ω is in revolutions per minute and r in cm.)

relative density *symbol*: d; the ratio of the mass density of a substance, ρ, at a given temperature, to the mass density of a reference substance (usually water), ρ° at a reference temperature (usually 4 °C); i.e. $d = \rho/\rho^\circ$.

relative formula mass the relative molecular mass as calculated from the formula of a compound.

relative molecular mass *or* **relative molar mass** *or* **molecular weight** *abbr.*: r.m.m.; *symbol*: M_r; the ratio of the mass of a molecule, m_f, to the atomic mass constant, m_u, which is one-twelfth of the mass of the nuclide ^{12}C; i.e. $M_r = m_f/m_u$. M_r is a mass ratio, a pure number with no units. The convention for indicating the size of a protein is thus 'M_r' followed by a number without units, e.g. M_r 10 000; the equivalent **molecular mass**, i.e. its mass in daltons, would be 10 kDa. *See also* **dalton**, **relative atomic mass**, **unified atomic mass unit**.

relative permittivity *symbol*: ε_r; *formerly called* **dielectric constant**, the ratio of the permittivity of a substance, ε, to the permittivity of vacuum, ε_0, i.e. $\varepsilon_r = \varepsilon/\varepsilon_0$.

relaxation *(in chemistry)* the process of self-adjustment of a molecular system to a new state of minimum free energy following a disturbance.

relaxation kinetics a technique used to study rapid reactions in which a mixture at equilibrium is rapidly adjusted to a new set of conditions. The system is then observed as it approaches its new equilibrium, a process known as **relaxation**. The temperature-jump method is often used, whereby an electric discharge is used to increase the temperature by several degrees in a period of about 1 μs. *See also* **rapid-reaction kinetics**.

relaxation spectrometry the use of spectrometry to follow the kinetics of a reaction undergoing relaxation from a perturbation. *See* **relaxation kinetics**.

relaxed control a mechanism of control of plasmid replication in which replication of plasmids greatly exceeds that of the chromosome. *Compare* **stringent control**.

relaxed DNA circular DNA that is not supercoiled (*see* **supercoil**), and instead has an unwound loop. The supercoiled form is energetically favoured over the relaxed form. Since the supercoiled DNA is more compact it moves faster when centrifuged or upon electrophoresis, and so the two forms of DNA can be separated.

relaxed form *abbr.*: R form; one of two alternative quaternary structures of a protein, the other being the **tense form** (or taut form, *abbr.*: T form). These forms derive from the concept of two conformational states of a protein, which differ in their affinities for a ligand. Factors affecting the conformational equilibrium also influence the affinity of ligand-binding and vice versa. Such factors may include the ligand itself, which could enhance or reduce the affinity of the protein, giving rise to **positive cooperativity** or **negative cooperativity** of binding respectively. The T form has a lower affinity for the substrate. For example, oxyhemoglobin is R, and deoxyhemoglobin is T; the binding of O_2 to the heme group causes the iron atom to move with respect to the heme plane, and this favours the move from T to R. *See also* **allosteric constant**, **Monod–Wyman–Changeux model (for allosteric compounds)**.

relaxed mutant a bacterial *mutant* that lacks the *rel* (*relaxed*) gene, which exerts a critical control over the **stringent response**. The *rel*$^-$ mutant is unresponsive to amino-acid starvation, so that rates of RNA synthesis, for example, continue as before. *See also* ***relA***.

relaxin a protein hormone (M_r ≈5600) that is responsible in most mammals (including humans) for dilation of the symphysis pubis, softening of the cervix, and various other physiological changes prior to parturition. It is synthesized and stored in the corpus luteum. Like **insulin**, the hormone consists of two polypeptide chains linked by two disulfide bonds, with an intrachain disulfide bridge also present. Although otherwise dissimilar in primary structure, the two proteins have very similar tertiary structures. As with insulin, synthesis is thought to occur via an inactive, single-chain precursor, in this case **prorelaxin**, and storage is as granules in vesicles. Example from human (precursor): database code REL1_HUMAN, 185 amino acids (21.12 kDa). *See also* **insulin-related growth factors**.

release factor *abbr.*: RF *or (formerly)* R factor; proteins that participate in the release of a nascent polypeptide chain from a ribosome. There are two classes of release factors, one codon-specific and the other non-codon-specific. In bacteria two codon-specific factors have been identified, RF-1, specific for UAG/UAA, and RF-2, specific for UGA/UAA. In eukaryotes one such factor has been found, eRF-1. These factors act at the ribosomal A-site and require polypeptidyl-tRNA at the P-site. In bacteria the action of RF-1 and RF-2 are aided by the non-codon-specific RF-3 which binds to guanine nucleotides. In eukaryotes a similar factor, eRF-3, has been identified. The genes encoding RF-1 (*prfA*) and RF-2 (*prfB*) have been identified. Mutations in these genes often cause misreading of termination signals, increased frameshifting, and temperature-sensitive growth of the cells. Examples from *Escherichia coli*: RF-1, database code RF1_ECOLI, 360 amino acids (40.41 kDa); RF-2, database code RF2_ECOLI, 365 amino acids (41.19 kDa). *See also* **ribosome recycling factor**.

release-inhibiting factor *or* **release-inhibiting hormone** any polypeptide that inhibits the release of a hormone or hormones. An example is **somatostatin**.

releasing hormone *or* **releasing factor** any of a group of peptide neurohormones that are synthesized in various distinct regions of the hypothalamus. They are released in nanogram amounts into the capillaries of the portal vessels of the median eminence of the hypothalamus, then carried to the anterior pituitary where they regulate the production and secretion in microgram amounts of the tropic hormones, e.g. thyrotropin, somatotropin, and the gonadotropins. In the anterior pituitary they act via the **adenylate cyclase** system and are then degraded by proteolysis.

rem *symbol*: rem; a non-SI unit of (radiation) **dose equivalent**, equal to 0.01 J kg^{-1} of irradiated human (or other mammalian) tissue. It is being superseded by the **sievert**; 1 rem = 10^{-2} sievert. [Acronym for röntgen equivalent man (or mammal).]

REMI *abbr. for* restriction enzyme-mediated integration (*see* **insertational mutagenesis**).

remnant a fragment of a molecule or other entity remaining after partial degradation especially **chylomicron** remnant.

renal pertaining to, or of, the kidney.

renal rickets a condition occurring in older children and characterized by the skeletal changes of **rickets**, due to impairment of renal function allowing excessive loss of calcium and phosphate into the urine.

renaturation the return of denatured macromolecules (protein, DNA, etc.) to the conformation they maintained before denaturation. In the case of proteins, reversible denaturation is brought about by disulfide reducing agents and urea, for nucleic acids by heat or salts. *See also* **native state**.

renewal (of tissue) *see* **regeneration** (def. 2).

renin *or* **angiotensin-forming enzyme** *or* **angiotensinogenase** EC 3.4.23.15; a labile proteolytic enzyme, M_r ≈40 000, formed from prorenin in plasma and kidney, and secreted into the blood by the kidney. It is also produced in relatively large amounts by the submaxillary gland of certain strains of mice. A glycoprotein aspartic endopeptidase, it is highly specific for the Leu-|-Leu bond in **angiotensinogen**, which it cleaves to generate angiotensin I. Despite its high specificity it resembles other eukaryotic aspartyl proteinases. Example, precursor from human: database code RENI_HUMAN, 406 amino acids (45.01 kDa). It is a **preproprotein**; residues 1–23 are the peptide signal and 24–66 are the propeptide. 3-D structure is known. *Compare* **renin**.

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renin–angiotensin system a system involved in the control of blood pressure. **Renin**, secreted into the blood by the kidney in response to osmotic changes, anoxia, or kidney trauma, acts on angiotensinogen to release angiotensin I (AI) (*see* **angiotensin**). **Angiotensin-converting enzyme** forms angiotensin II (AII) from AI by release of His–Leu from the C-terminal end. AII stimulates release of the mineralocorticoid **aldosterone** from the glomerulosa cells of the adrenal cortex. Various nonapeptide analogues of AI inhibit converting enzyme and are used in the treatment of renin-dependent hypertension. *See also* **captopril**.

rennet an extract obtained from the stomachs of young mammals living on milk. It contains rennin (i.e. **chymosin**), an enzyme that clots milk and is used in cheese-making.

rennin *an alternative name for* **chymosin** (which is preferred because of possible confusion with **renin**). *See also* **rennet**.

Reoviridae a family of double-stranded RNA viruses (class III in the **Baltimore classification**) with a segmented genome, infecting vertebrates, arthropods, and plants. The virion consists of a nonenveloped icosahedral particle, 60–80 nm across, and containing 10–12 segments of RNA together with **RNA-directed RNA polymerase**; the latter serves to transcribe the negative strand of each RNA molecule into mRNA. This family comprises six groups: the orthoreoviruses, orbiviruses, rotaviruses, cytoviruses, phytoreoviruses, and Fijiviruses. No pathology is associated with the orthoreoviruses infecting humans, but rotaviruses cause gastroenteritis, and orbiviruses cause the disease blue tongue in sheep.

reovirus *see* **Reoviridae**.

rep an obsolete unit of **absorbed dose** of **ionizing radiation** of any kind, equal to the dose of radiation that, upon absorption by a given mass of living tissue, causes the same energy deposition as 1 röntgen of X- or gamma radiation, i.e. about 96 ergs per gram (0.0096 J kg^{-1}) of tissue. *See also* **rad**, **rem**. [Acronym for röntgen equivalent physical.]

REP *abbr. for* repetitive extragenic palindromic sequence.

RepA the protein product of the *Escherichia coli* gene *repA* which has a role in the replication of DNA in *E. coli*. Although the principal **DNA helicase** in *E. coli* is DnaB helicase, there is also a different 68 kDa monomeric protein, which has some helicase activity during certain life-cycle stages of the replication of single-stranded phages. The contribution of RepA protein to the host cell is less clear, but the rate at which *E. coli* replication forks propagate is reduced in rep^- mutants.

repairase an enzyme concerned in the repair of an interrupted polynucleotide chain.

repair enzyme any of the enzymes making up the enzyme complex responsible for the excision of **pyrimidine dimers** which are formed on exposure of DNA to ultraviolet light, when adjacent pyrimidine residues on a DNA strand become covalently linked. Three enzymic activities are essential for the repair: (1) an enzyme complex comprising the three proteins encoded by the *uvrABC* genes (*see* ***uvr***) that detects the distortion produced by the pyrimidine dimer: (2) the UvrABC enzyme complex also has another activity, described as a specific excinuclease, which cuts the damaged DNA strand eight nucleotides away from the dimer on the 5′ side and four nucleotides away on the 3′ side; (3) the 12-residue oligonucleotide excised by this specific excinuclease diffuses away and DNA polymerase I enters the gap to effect repair synthesis. Gaps are filled by **DNA ligase**. *See also* **DNA repair enzyme**, **excision repair**, **recombinational repair**, **mismatch repair**.

repeated genes *see* **repetitive sequences**.

repeat-induced point (mutation) *see* **RIP**.

repeat sequence *or* **repeat** **1** *(in DNA) see* **repetitive sequences**. **2** *(in proteins)* any sequence of the same amino-acid residue or group of amino-acid residues that is repeated in a polypeptide. Thus in some cases there are runs of glutamine or cysteine. In *Drosophila melanogaster* there is a protein with a string of 11 cysteine residues, and human androgen receptor protein has a string of 21 glutamine residues. In fact there are at present in composite databases 44 proteins with this number of glutamine residues. In other proteins, e.g. tropocollagen, there is a regular sequence, except in this case for the last 20 amino-acid residues at each end of the chain. In tropocollagen every third residue is glycine usually followed by proline or hydroxyproline. The intrachain hydrogen bonds involve glycine. **3** the repeats of sugar residues often found in complex polysaccharides.

repeat unit a major periodicity in the structure of a molecule as deduced from X-ray diffraction patterns.

repetitive extragenic palindromic sequences *or* **palindromic units** palindromic sequences in repetitive DNA in *Escherichia coli* and *Salmonella typhimurium*. These are never found within a coding sequence. They are topoisomerase substrates and potential transcription terminators.

repetitive sequences repeated sequences of nucleotides found in the DNA of eukaryotes. There are various types. (1) **Satellite DNA** typically consists of tandem (head-to-tail) repeats of a few hundred nucleotides. It is so called because those first discovered had an unusual ratio of bases that made it possible to separate the satellite DNA from the bulk of the cell DNA in a centrifuge. (2) **Minisatellite** DNA consists of shorter tandem repeats. The **restriction fragment length polymorphisms** linked to many genes have short sequences of bases in common. rDNA (*see* **ribosomal DNA**) probes for these sequences are useful in the preparation of a profile of the genome of an individual (fingerprinting). (3) **Transposons** (transposable elements) are also characterized by repeated sequences, often numbering several hundred copies. Primate DNA has large numbers of two types of transposable elements, L1 transposable elements and **Alu sequences**, which comprise about 300 bases. (4) **Repeated genes** for rRNA and histones are also found. In many cases repetitive sequences seem to be maintained solely by their ability to replicate within the genome (the '**selfish DNA hypothesis**'). Rather than conferring benefits their behaviour can sometimes result in loss of fitness to the host, as in some human genetic diseases; mutations can arise due to insertion of transposable elements, to chromosomal rearrangements induced by recombination between repeated sequences, or to amplification of microsatellite sequences.

replacement vector a **cloning vector** in which part of the normal genome is replaced by foreign DNA. It contrasts with an **insertion vector** where the foreign DNA is merely incorporated into the normal genome. For example, a mutant of lambda phage, called λgt-λβ, contains only two *Eco*RI cleavage sites and so the middle segment of the DNA can be removed leaving 72% of the normal genome. A suitably long DNA replacement between the two ends of lambda DNA enables such a recombinant DNA molecule to be packaged into a lambda particle.

replica *(in electron microscopy)* a reproduction of the surface of an object. There are various ways by which the surface of an object, e.g. membrane of an organelle, may be examined by transmission electron microscopy by means of a replica. Such a replica may be obtained by evaporating a thin film of a heavy metal such as platinum on to the dried specimen. The metal is sprayed from an oblique angle in order to deposit a coating of uneven thickness because a shadow effect is created that gives the image a three-dimensional appearance. The organic material may be dissolved away to provide a replica of the surface of the specimen. Two other methods, **freeze-etching** and **freeze-fracturing**, employ frozen sections.

replica plating a technique for the production of identical patterns of bacterial colonies on a series of agar plates. The method uses velveteen or other fabric stretched on a pad, which is then pressed onto a plate of bacterial cultures so that some bacteria from each colony are transferred to the pad, preserving the spatial pattern of the colonies (in mirror image). If this pad is then pressed lightly onto a fresh culture plate, it will transfer colonies in the same formation to the new plate. This new plate may be prepared using media that will be selective for certain mutants, fermentation reactions, or anti-

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biotic sensitivity. A similar technique can be used in the screening of **hybridomas** for antibody production.

replicase *a loose term for* certain polymerase enzymes; e.g. certain viral **RNA-directed RNA polymerases** can be referred to as RNA replicases.

replicate **1** to make an exact copy of something, as in the **replication of DNA**. **2** *(in electron microscopy)* to make a **replica**.

replication complex the complex of replication proteins that are linked together as a single large unit, of total mass 10^6 daltons, that moves rapidly along the DNA during **replication of DNA**. It enables DNA to be synthesized on both sides of the replication fork in a coordinated and efficient manner. That part of the complex that contains **DNA primase** and **DNA helicase** is known as the **primosome**.

replication-error mutation a mutation that arises during DNA replication as a result of the incorrect copying of the sequence of nucleotides in the parent DNA. Probably fewer than one mistake occurs in 10^9 nucleotides added.

replication fork *or* **replicating fork** the Y-shaped region of a replicating DNA molecule or chromosome, resulting from separation of the DNA strands and in which synthesis of new strands takes place. The process requires the participation of **helicases** that open the duplex.

replication of DNA the means whereby new strands of deoxypolynucleotides are synthesized. The structure of double-stranded DNA, with two strands of complementary base pairs, led Watson and Crick to propose a possible means of copying DNA: the two strands could unwind and each act as the template for a new strand, thus forming two helices, each containing one parental strand and one new one. The elegant **Meselson–Stahl experiment** demonstrated that DNA replication was indeed semiconservative. Other mechanisms of replication, 'conservative' and 'dispersive', have been proposed but there is no evidence that they occur. The helix of the double-stranded parental DNA must be unwound and this requires more than 20 proteins in a complex known as a **primosome**. All DNA-dependent DNA polymerases synthesize the new strands in the direction 5′ to 3′ using as substrates deoxynucleotide triphosphates with the production of pyrophosphate. The new strands are antiparallel to the parental template strand. At low resolution both strands of a double-stranded DNA appear to be synthesized in the same direction in spite of the fact that the polymerases only synthesize the strands in one direction. The problem is resolved by the fact that one strand, the **leading strand** (*or* continuous strand), is synthesized in a continuous fashion whereas the other strand, the **lagging strand** (*or* discontinuous strand), is synthesized discontinuously to give **Okazaki fragments** (1000–2000 nucleotides long in prokaryotes and 100–200 nucleotides long in eukaryotes) which are eventually joined by **DNA ligase**. The DNA ligases cannot start a chain and must rely on a priming device which is provided by RNA **primase** which again synthesizes an RNA primer in the direction 5′ to 3′ using nucleoside triphosphates as substrate. The continuous strand needs to be primed only once whereas the discontinuous strand must be primed repeatedly. Three principal **DNA polymerases** for *Escherichia coli* were discovered in the laboratory of A. **Kornberg**. **DNA polymerase I**, in addition to possessing synthetic activity *in vitro*, is also a 3′–5′ **exonuclease** which gives it an editing function. It also has 5′–3′ nuclease activity. **DNA polymerase II** participates in DNA repair but is not required for replication. **DNA polymerase III** is the predominant polymerase for replication of *E. coli* DNA *in vivo*. Eukaryotic cells have at least four DNA polymerases.

replicative able to be replicated. *See also* **replicative form**.

replicative form *abbr.*: RF; the intracellular form of viral nucleic acid that is active in replication. A single-stranded viral nucleic acid, be it RNA or DNA, is first converted into a double-stranded form – the **replicative intermediate** – to enable the viral strand to be replicated preferentially. In the case of a **retrovirus** a hybrid of RNA and DNA is formed.

replicative intermediate *see* **replicative form**.

replicon **1** a structural gene that controls the initiation and replication of DNA. **2** by association, the whole DNA sequence (such as the bacterial chromosome) that is replicated under the influence of a single replicon system.

replisome a **replication complex** hypothesized to account for the initiation of chromosome replication within a living cell.

replitase a particulate fraction that can be isolated from the nuclei of **S phase** Chinese hamster embryo fibroblasts and containing some of the enzyme activities required for DNA synthesis.

reporter gene a gene used to disclose the function of potential regulatory sequences. The sequences are placed in plasmids, upstream of the reporter gene; these chimeric plasmids are then introduced into cells and the expression of the reporter gene is measured as an index of the function of the regulatory sequences under the conditions being investigated. The *lacZ* (**β-galactosidase**) gene, the *CAT* gene (*see* **chloramphenicol *O*-acetyltransferase**), and the gene encoding firefly **luciferase** have been used in this way.

reporter group a chemical group that acts as a **probe**.

repress to check or restrain; the effect may be partial or total. *See* **repression**, **repressor**.

repressible describing a metabolic reaction that is capable of undergoing **repression**.

repression *(in genetics)* the act of inhibiting gene expression. An example is **catabolite repression** of the *lac* operon by glucose, mediated through binding of cyclic AMP to **catabolite (gene) activator protein** (CAP). By extension, the gene product itself (enzyme or other protein) and thus any associated metabolic reaction is said to be repressed. *See also* **repressor**.

repressor *(in genetics)* a molecule that specifically prevents the transcription of regulatory genes under control of an **operator**. When the repressor is bound to the operator, transcription cannot occur. An inducer can induce transcription by binding to the repressor to form a complex that has a low affinity for the operator. The classic example of a repressor is the lactose repressor protein, which controls the expression of the ***lac* operon** in *Escherichia coli*. The protein binds to a specific sequence of 21 nucleotide pairs (called the operator) that overlaps an adjacent RNA polymerase binding site (the promoter) at which RNA synthesis begins. In the presence of lactose, allolactose is formed, which binds to the repressor. This induces a conformational change that causes the repressor to loosen its hold on the DNA so that the gene is derepressed. In other examples, the binding of a signalling molecule may increase the affinity with which the repressor binds to the DNA; e.g. the *trp* operon, encoding enzymes that produce tryptophan in *E. coli* (*see* **trp gene**). *See also* **repression**.

reproducibility the ability to carry out a series of identical experiments to yield results that fall within a small range of error derived by statistical analysis (*see* **standard deviation**, **standard error of the mean**). The limits of error that are acceptable depend on the limitations of experimental technique and the inherent variability of the system under investigation.

reproduction *(in biology)* the production by an organism of new individuals that are more or less similar to itself. Reproductive strategies can be divided broadly into two categories: sexual reproduction, which requires the participation of male and female **gametes** and gives rise to genetic variation among the offspring; and asexual reproduction, which does not involve gametes and leads to the formation of offspring that are genetically identical to the parent. The latter takes various forms; examples include **budding**, **fragmentation**, **parthenogenesis**, **spore** formation, and **vegetative reproduction**.

reptation a term invoked to rationalize the movement and thermodynamics of linear polymers, dividing the chain conceptually into sections (**reptons**), which form the basis for statistical mechanical calculations of the relaxation time of the polymer and viscosity of polymer solutions.

repton *see* **reptation**.

RER *abbr. for* rough endoplasmic reticulum.

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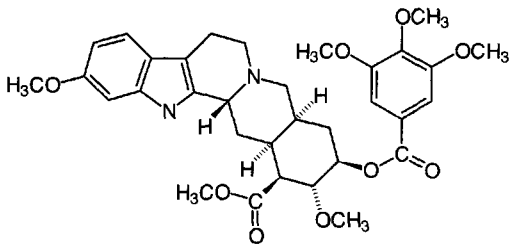
reseal to join again the ends of ruptured components, as in, e.g., the resealing of plasma membranes after whole cells have been rendered permeable by various techniques, or of fractionated membrane fragments, which may reseal to form closed vesicles. The term can also refer to ligation of the cut ends of DNA after insertion of foreign DNA into a vector.

reserpine ($3\beta,16\beta,17\alpha,18\beta,20\alpha$)-11,17-dimethoxy-18[(3,4,5-trimethoxybenzoyl)oxy]yohimban-16-carboxylic acid methyl ester; an alkaloid isolated from the roots of certain species of *Rauwolfia* and noted for its antihypertensive and CNS depressant actions. These arise from its inhibition of the intraneuronal Na^+, Mg^{2+}-ATPase pump, which maintains the neuronal vesicular stores of biogenic monoamines (**dopamine**, **norepinephrine**, and **serotonin**).



reserve polysaccharide any polysaccharide that is stored to provide an energy source at times of need. Examples are starch granules in plants, and glycogen granules in animals.

***Re/Si* convention** a nomenclatural system for specifying the **stereoheterotopic** faces of a trigonal atom using the **sequence rule** in two dimensions. This is used to establish a priority sequence for the three ligands, e.g. of *Cabc*. The plane containing C and the first atoms of the ligands is then inspected from an arbitrarily chosen side. Starting with the highest priority ligand, it is determined whether the priority sequence is clockwise, hence *Re* (from Latin *rectus*, right), or counterclockwise, hence *Si* (from Latin *sinister*, left); e.g. for acetaldehyde, CH_3CHO, if the face inspected shows a clockwise ordering, $O \rightarrow CH_3 \rightarrow H$, that face is designated *Re*. There are a number of extensions of this general principle, and the specialist literature should be consulted for details.

residence time the averaged time that a site is occupied by any designated molecule.

resident protein *see* **luminal protein**.

residual body a membrane-lined cytoplasmic inclusion characterized by undigested residues (e.g. membrane fragments or whorls, ferritin-like particles). The term embraces **telolysosome** and (hypothetical) **post-lysosome**.

residue **1** any of the incorporated amino-acid moieties in a peptide or protein. **2** material that remains after any procedure to remove something.

residue mass the relative molecular mass of a residue; i.e. the sum of the **relative atomic masses** of all the atoms composing the residue.

residue weight the molecular weight of a residue; i.e. the sum of the **atomic weights** of all the atoms composing the residue. **Residue mass** is the preferred term.

resin **1** *or* **rosin** any of a group of naturally occurring amorphous solids or semisolids, typically light yellow to dark brown in colour. Usually brittle and insoluble in water, they are found as plant exudates, often on trees such as pines and firs. **2** the polystyrene base of certain ion-exchange materials used in chromatography. The polystyrene is modified to carry sulfonic acid or carboxyl groups (cation exchangers), or primary or quaternary ammonium groups (anion exchangers).

resistance **1** the ability of a living organism, particularly a bacterium, to resist the effect of a disadvantageous environment or substance, especially an antibiotic. A bacterium may possess one or more resistance plasmids. **2** *see* **electric resistance**.

resistance donor a strain of an organism, usually a bacterium, that is capable of transferring resistance, usually by conjugation, to a suitable recipient.

resistance factor *abbr.*: R factor; *an alternative name for* **resistance plasmid**.

resistance plasmid *abbr.*: R plasmid; a **plasmid** that carries genetic information for resistance to antibiotics or other antibacterial drugs. *Other name*: resistance factor (*abbr.*: R factor).

resolution **1** the degree of separation between two compounds being subjected to a transport method such as chromatography or sedimentation equilibrium (i.e. being resolved); complete resolution yields two compounds each uncontaminated by the other. **2** *(in physics and biophysics)* the extent to which closely juxtaposed objects can be distinguished as separate objects using an optical instrument, e.g. a microscope. The degree of resolution is dependent on the **resolving power** of the system. The fineness of detail with which objects can be seen is limited by the wavelength of light used. Only those objects similar in dimensions to the wavelength of the light (or larger) can be resolved. The wavelength of X-rays is from about 10^{-8} m to 10^{-11} m and they can thus be used to resolve structures at the atomic level. Thus a structure can be said to have been determined at 3 Å resolution, 7 Å resolution, etc.

resolvase an enzyme that, together with **transposase**, is involved in the replicative transposition of genetic elements in *Escherichia coli*. The 3′ ends of the target chromosome, after the first cutting and splicing, serve as replicative primers for copying both the gaps and the two strands of the transposable element (which contains transposase) itself. Ligase action generates a cointegrate, a large circular structure containing both donor and target chromosomes with two freshly replicated copies of the transposable element. Resolvase now catalyses the site-specific recombination between the two elements, resulting in one copy of the transposable element inserted in each of the two chromosomes. Example, *tnpA* gene product from Tn3 which confers resistance for ampicillin; database code TNP3_ECOLI, 185 amino acids (20.59 kDa); it contains a **helix-turn-helix** motif.

resolving power **1** *(in chromatography)* the power to resolve individual compounds (*see* **resolution** (def. 1)). It depends on (1) the efficiency of the system employed; for columns this is given by the **theoretical plate** number; and (2) the relative affinities of different compounds for the stationary and mobile phases. **2** *(in physics)* **a** the ability of an optical instrument, e.g. a microscope or telescope, to produce separate images of objects placed close together. **b** the ability of a spectrometer to separate adjacent peaks in a spectrum.

resonance **1** *(in physics)* the induction or amplification of one vibration by another vibration of a periodicity equal to the natural oscillation frequency of the first, which is then said to resound. In an electronic circuit, resonance occurs when an applied emf equals the natural frequency of oscillation of the circuit (used, e.g., in tuning a radio receiver). **2** *(in chemistry)* a phenomenon shown by any molecular entity to which more than one **contributing structure** can be assigned, when these structures are of similar energy and differ only in the distribution of the valence electrons; the entity then oscillates between the two structures and adopts, in effect, an intermediate state. Resonance always results in a different distribution of electrons than would be the case if there were no resonance. *See also* **resonance energy**, **resonance hybrid**. **3** *see* **electron spin resonance spectroscopy**, **nuclear magnetic resonance**. —**resonant** *adj.*; **resonate** *vb.*

resonance energy the difference in energy of an actual molecule and the **contributing structure** of lowest energy.

resonance hybrid the structure that results when a chemical entity exhibits **resonance** (def. 2), such as occurs by the sharing of one or more electrons over several bonds. It has a lower en-

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ergy than any of the possible formal nonresonance **contributing structures**, giving additional stability of which the so-called **resonance energy** is a measure. A classic example is carbon dioxide, which may be represented by the **Lewis formula** for each as Ö::OC::Ö, ⁻Ö:C:::O⁺, and ⁺:O:::C:Ö:⁻. *Compare* **mesomerism**.

resonance stabilization *or* **resonance stabilisation** stabilization of molecular structure by resonance; *see also* **resonance hybrid**.

resonate *see* **resonance**.

resorb to absorb again. —**resorbent** *adj.*; **resorption** *n.*; **resorptive** *adj.*

resorcinol *m*-dihydroxybenzene; a compound used in the **Seliwanoff test** for ketoses.

resorption *see* **resorb**.

respiration **1** the process of gaseous exchange between an organism and its environment. In plants, microorganisms, and many small animals, air or water makes direct contact with the organism's cells or tissue fluids, and the processes of diffusion supply the organism with dioxygen and remove carbon dioxide. In larger animals the efficiency of gaseous exchange is improved by specialized respiratory organs, such as lungs and gills, which are ventilated by breathing mechanisms. These organs possess respiratory surfaces, across which gases are exchanged with the blood or other transport medium. This then carries dioxygen to the body tissues, and removes carbon dioxide. **2** *or* **oxidative metabolism** the various energy-yielding reactions of cells or organisms that require oxygen as the final electron acceptor. *See* **respiratory chain**. —**respiratory** *adj.*

respiratory burst a phase of elevated metabolic activity, during which oxygen consumption increases, that occurs in neutrophils, monocytes, and macrophages shortly after phagocytosing material. This is associated with increased activity of the hexose monophosphate shunt and production of **NADPH** (*see* **pentose phosphate pathway**). An oxidase takes electrons from the NADPH and transfers them to O_2 creating the reactive superoxide (O_2^-) ion and H_2O_2 in the vacuole. Patients with chronic granulomatous disease never produce a respiratory burst. In some cases this is due to lack of an essential cytochrome *b*. The patients suffer an accumulation of mononuclear cells at sites of chronic inflammation, forming granulomas.

respiratory chain *or* **electron-transport chain** the sequence of enzymes and other proteins within the mitochondrion and prokaryotic cell membranes by which substrates, including NADH and succinate, are oxidized by dioxygen. It is fundamental to tissue **respiration** (def. 2) which has the function of maintaining tissue metabolism through **oxidative phosphorylation**. The chain can be separated into a number of particles (*see* **respiratory complex**) each of which contains individual elements of the chain. The mechanism involves, in the case of NADH, removal by NADH dehydrogenase of a proton plus two electrons. In the case of succinate, there is a transfer of two hydride ions (i.e. two protons plus two electrons) by succinate dehydrogenase to the enzyme-bound FAD; other flavoproteins can similarly oxidize fatty acyl-CoA or β-hydroxybutyrate or α-glycerophosphate. The protons are initially released to the intermembrane space, and the electrons are transferred by the appropriate flavoprotein to ubiquinone, from which they are transferred singly in sequence to cytochrome *b*, cytochrome c_1, cytochrome *c*, and cytochrome a/a_3 at which point they reduce molecular oxygen to promote formation of water with the protons that were formed earlier. Many other components are also involved. In tightly coupled mitochondria, the protons released to the intermembrane space reach the mitochondrial matrix (the space in which they react with molecular oxygen) by transfer through the inner mitochondrial membrane by the F_0F_1 complex of the mitochondrial ATPase (*see* **H⁺-transporting ATP synthase**), with concomitant phosphorylation of ADP to ATP. *See also* **chemiosmotic coupling hypothesis**.

respiratory complex any of several groups of physically associated components of the **respiratory chain**. The concept arose during experiments to purify individual components, when it was found that membrane particles could be isolated each with a consistently characteristic composition. Four main complexes have been identified: complex I, which contains primarily NADH dehydrogenase; complex II, which contains succinate dehydrogenase; complex III, which contains cytochromes *b* and c_1; and complex IV, which contains cytochrome a/a_3 together with copper-containing proteins. Complexes I, II, and III all contain additionally a number of proteins rich in iron and sulfur. The F_0 and F_1 subunits of the ATPase associated with the respiratory chain have been termed complex V (*see* **H⁺-transporting ATP synthase**). *See also* **complex I, II, III, IV**.

respiratory control the regulation, in coupled mitochondria, of the rate of oxidative phosphorylation by the level of ADP. As the ADP level increases, and the ATP level falls, electron flow through the **respiratory chain** and coupled ATP synthesis are enhanced. The **respiratory control ratio**, or **respiratory control index**, represents the ratio of the rate of oxygen consumption of mitochondria in the presence of both substrate and ADP to the rate in the presence of substrate but the absence of ADP; i.e. the ratio of the rate in respiratory state 3 to respiratory state 4 (*see* **respiratory state**).

respiratory pigment any of a number of pigmented proteins, associated with respiratory processes, that derive their colour from a prosthetic group, usually heme in red proteins such as cytochrome *c*, or flavin nucleotides in flavoprotein dehydrogenases, which are yellow.

respiratory quotient *or* **respiratory ratio** *abbr.*: RQ; a ratio of the rate of carbon dioxide evolution by any cell, tissue, or organism to its rate of dioxygen uptake.

respiratory state *or* **state of the respiratory chain** any one of the possible steady states of the phosphorylating **respiratory chain** in mitochondria. In state 1 both ADP and respiratory substrates are lacking. State 2 is a 'standard state' in which ADP has been added to exhaust the endogenous respiratory substrate; in state 2′ substrate has been added to exhaust the endogenous ADP. In state 3, the 'active' state of rapid respiration, all required components are present and the respiratory chain itself is the rate-limiting factor. State 4, an anaerobic 'resting' state, is characterized by a low respiration rate. In state 5, only oxygen is lacking, the respiration rate then being at zero.

State	$[O_2]$	[ADP]	Substrate level	Respiration rate	Rate-limiting factor
1	>0	low	low	slow	ADP
2	>0	high	0	slow	substrate
2′	>0	low	high	slow	ADP
3	>0	high	high	fast	respiratory chain
4	>0	low	high	slow	ADP
5	0	high	high	0	O_2

respirometer an instrument for measuring the uptake of oxygen during incubation experiments. The **Barcroft apparatus** and the **Warburg apparatus** were examples of this type of instrument.

response the events brought about by a **stimulus**, especially in a cell, tissue, or organism. *See* **stimulus–response coupling**, **sensitization**, **desensitization**.

response coefficient *symbol*: *R*; an overall measure of the control exercised by a specific enzyme inhibitor, at its concentration, *I*, on the overall flux, *F*, of a multienzyme system. Hence,

$$R_I^F = (\partial F/F)/(\partial I/I)$$

or

R = fractional change in flux/fractional change in inhibitor.

A response coefficient can also be determined for the effect of *I* on the concentration of a metabolite *S*. Thus

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$$R_I^S = (\partial S/S)/(\partial I/I)$$

It is the product of the **elasticity coefficient** and the **flux control coefficient**.

response element *abbr.*: RE; a DNA sequence (sometimes called a 'module') that is common to promoters/enhancers of genes whose expression is coordinately regulated (*see* **coordinate induction/repression**). Examples: the **estrogen response element** (ERE) has the consensus sequence GGTCANNNTG[A/T]CC; the glucocorticoid response element (GRE) has the consensus sequence TGGTACAAATGTTCT; the **heat-shock response element** (HSE) has the consensus sequence GNNGAANNTCCNNG; the **metal response element** (MRE) has the consensus sequence CGNCCCGGNCNC; the **serum response element** (SRE) has the consensus sequence CATATTAGG; and the **thyroid response element** (TRE), which is common to several enhancers, has the consensus sequence TGACTCA.

response time the interval between initiation of a process and the commencement of the action that it induces.

responsiveness *(in physiology)* the ability of a cell, tissue, or organ to undergo a response. Maximal response normally corresponds to the healthy *in vivo* state, so that the degree of response is an indication of the integrity of the preparation. However, negative regulators may be removed during tissue preparation, thus giving enhanced activity *in vitro*.

restin Reed–Sternberg cell intermediate filament-associated protein; *other name*: cytoplasmic linker protein-170 α-2 (*abbr.*: CLIP-170); a protein that is highly expressed in such cells in Hodgkin's lymphoma and having a large coiled-coil α-helical domain similar to those in myosins. Example from human: database code REST_HUMAN, 1427 amino acids (160.81 kDa).

resting potential the potential difference across the membrane of a cell in the unstimulated state. *See also* **membrane potential**.

resting state an inactive or unstimulated state, especially of a cell. *See also* **cell-division cycle**.

restricted DNA DNA that has been cut by a **restriction endonuclease** within a bacterium; bacteria are protected from the propagation within them of foreign DNA, usually viral DNA, by the possession of restriction endonucleases which degrade the invading DNA. Each nuclease recognizes a specific sequence of 4–8 nucleotides in the DNA. The cleaved sequences, where they occur in the genome of the bacterium itself, are protected from cleavage by methylation at the amino group of an adenine, or either the 5 position of a cytosine or the amino group of a cytosine. The newly replicated strand of the bacterial host DNA, which is protected from degradation by the methylated parent strand with which it forms a duplex, is modified before the next cycle of replication (*see* **restriction–modification system**). Such sequences in the viral DNA are usually not so methylated and hence are degraded first by the restriction enzymes and then by bacterial exonucleases. Invading DNAs are only rarely modified and enabled to reproduce in their new host. Its progeny are, however, no longer modified in the way that permits them to propagate. *See also* **host-controlled modification**.

restricted phage *or* **restricted bacteriophage** *see* **restricted virus**.

restricted virus a virus whose host range is limited by **host-controlled modification** so that when it infects a related but non-identical host cell its DNA is degraded by the new host cell's **restriction endonucleases**.

restriction *(in molecular biology)* the action or use of **restriction endonucleases**. *See also* **restrictive**.

restriction analysis *another term for* **restriction mapping**.

restriction endonuclease *or* **restriction enzyme** *or* **restriction nuclease** any of a group of enzymes, produced by bacteria, that cleave molecules of DNA internally at specific base sequences. They, therefore, act to 'restrict' the replication of foreign, usually viral, DNA entering the bacterial cell (*see* **restricted DNA**). Some of them also methylate the host bacterial DNA to protect it from degradation. There are three known types of restriction enzymes. Types I and III each carry activity for both the endonuclease and methylase function whereas type II enzymes do not carry the methylase activity. Type I enzymes cleave the DNA at a random site located at least 1000 bp from the recognition sequence, type III do so 24–26 bp distant from the recognition site. In contrast type II enzymes cleave DNA at specific sites within the recognition sequence. This makes type II enzymes indispensable for DNA manipulation. Around 2500 species of type II restriction enzymes with some 200 differing sequence specificities have been characterized. A restriction endonuclease is named by the first letter of the genus of the bacterium that produced it and the first two letters of its species, followed by its serotype or strain designation, and a roman numeral if the bacterium contains more than one type of restriction enzyme. **Type I** (EC 3.1.21.3) restriction and modification enzymes are complex, multifunctional systems that require ATP, *S*-adenosyl methionine, and Mg^{2+} as cofactors; in addition to their endonucleolytic and methylase activities, they are potent DNA-dependent ATPases. The subunit composition, three subunits designated R, M, and S, is similar to that of ATPases. They catalyse the endonucleolytic cleavage of DNA to give random double-stranded fragments with terminal 5′-phosphates; ATP is simultaneously hydrolysed. Example, R protein from *Escherichia coli*, enzyme *Eco*R124/3: database code T1R1_ECOLI, 1033 amino acids (119.52 kDa). **Type II** enzymes have activity as site-specific deoxyribonucleases (EC 3.1.21.4), which catalyse the endonucleolytic cleavage of DNA to give specific double-stranded fragments with terminal 5′-phosphates; Mg^{2+} is a cofactor. Example from *E. coli*, enzyme *Eco*RV: database code T2E5_ECOLI, 244 amino acids (28.49 kDa). Such enzymes are the basis of **restriction mapping**. **Type III** enzymes have activity as site-specific deoxyribonucleases (EC 3.1.21.5). The protein has two subunits, products of the *res* (from 'restriction') and *mod* (from 'modification') genes; these are respectively, responsible for binding the system-specific DNA recognition site in the restriction and the methylation of one of the adenosyl residues in the recognition site. A list of restriction endonucleases is given in **Appendix F**. *See also* **restriction–modification system**.

restriction enzyme *an alternative name for* **restriction endonuclease**.

restriction fragment a fragment of DNA produced by the action of a **restriction endonuclease**. It usually refers to the product of a type II enzyme that recognizes specific base sequences in double-helical DNA and cleaves both strands of the duplex at specific sites.

restriction fragment length polymorphism *abbr.*: RFLP; **polymorphism** within a population of organisms of the size of the fragments of DNA produced as the result of the action of a type II **restriction endonuclease**. It results from a corresponding polymorphism of **restriction sites** in the genome, due to slight differences in base sequence between individual members of the population. RFLP is exploited in constructing physical maps of the genome, and widely used for localizing specific genes and detecting genetic differences between closely related individuals. The analysis of restriction fragments can reveal the presence of a mutation that may itself cause disease or be closely linked to one that does; for example, genetic diseases such as sickle-cell anemia, cystic fibrosis, and Huntington's diseasae can be detected by RFLP analyses. *See also* **restriction mapping**.

restriction map a pattern obtained as the result of **restriction mapping**.

restriction mapping the use of type II **restriction endonucleases** to cleave genomic or other DNA to produce a characteristic pattern of fragments. The fragments are resolved by gel electrophoresis and visualized. Every DNA molecule produces a unique pattern, which accords with the specificity of the particular restriction enzyme. By comparing the patterns ob-

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tained from two or more different DNAs, differences between closely similar DNA molecules, such as arise from mutations, may be detected. The use of DNA probes, such as rDNA, to identify particular fragments may often be of value.

restriction–modification system *any system whereby host* DNA is methylated to render it resistant to the action of the cell's **restriction endonucleases** (*see* **restricted DNA**); methylation involves the adenine or cytosine residues at the restriction sites. Several enzymes have been implicated in this action: (1) EC 2.1.1.72; *recommended name*: site-specific DNA-methyltransferase (adenine-specific); *other names*: N-6 adenine-specific DNA methylase; modification methylase; it catalyses a reaction between *S*-adenosyl-L-methionine and DNA adenine to form S-adenosyl-l-homocysteine and DNA 6-methylaminopurine. (2) Another type is EC 2.1.1.73; *recommended name*: site-specific DNA-methyltransferase (cytosine-specific); *other names*: C-5 cytosine-specific DNA methylase; modification methylase; it catalyses a reaction between *S*-adenosyl-L-methionine and DNA cytosine to form S-adenosyl-l-homocysteine and DNA 5-methylcytosine. Examples: (1) *Eco*RV methylase from *Escherichia coli*: database code MTE5_ECOLI, 298 amino acids (34.60 kDa); (2) *Eco*P15 *mod* gene product of a type III system (*see* **restriction endonuclease**); this methylates one of the A residues in 5′-CAGCAC-3′; it is a homotetramer: database code T3MO_ECOLI, 645 amino acids (74.22 kDa).

restriction negative describing an organism that does not contain any **restriction endonuclease**.

restriction site a sequence of bases in a DNA molecule that is recognized by a **restriction endonuclease**.

restrictive **1** describing a strain or line of cells that does not permit the replication of a particular viral DNA, and is thus resistant to infection. **2** describing a set of conditions, such as a temperature range, in which a mutant phenotype is expressed, thus limiting the growth of the organism or causing its death. *Compare* **permissive**. *See also* **conditional lethal mutation**, **temperature-sensitive mutation**.

restrictive conditions *see* **conditional lethal mutation**.

restrictive temperature *see* **temperature-sensitive mutation**.

restrictocin an antitumour polypeptide, M_r 16 000, from *Aspergillus* spp. It cleaves the large RNA of the eukaryotic 60S ribosomal subunit and inhibits protein synthesis in picornavirus-infected cells.

RET a human transforming oncogene derived through fibroblast transfection with T-cell lymphoma DNA. It encodes two forms of receptor tyrosine kinases of unknown ligand; the cytoplasmic oncogenic forms ($p76^{RET}$, $p81^{RET}$) are constitutively phosphorylated on tyrosine; they form homo- and heterodimers, and have autophosphorylation activity. A number of variants have been associated with multiple endocrine neoplasia and Hirschprung's disease. Example (precursor): database code RET_HUMAN, 1114 amino acids (124.32 kDa).

retentate *or* **dialysis residue** *or* **residue** *(in* **dialysis***)* the moiety of the dialysed material that has not traversed the membrane; the liquid containing this moiety (which may or may not still be entirely in solution). Some authorities prefer the term **non-diffusible material**.

retention coefficient *(in column chromatography)* the ratio of the **void volume** to the **elution volume** for a specific solute. It is a measure of the partition of the solute between the column material and the solvent, and is independent of column size.

retention time the time taken by a compound to traverse the length of a **gas–liquid chromatography** column. The retention time is a characteristic of each compound under defined conditions. It can be used to aid in identification within a series of homologues, e.g. fatty acids, which are characterized by their **carbon number** derived from the retention time.

retention volume a parameter of liquid chromatography, related to the volume at which each compound elutes under defined conditions.

reticulate **1** *or* **reticular** resembling a net; in the form of a network. **2** to create in the form of a net or network. —**reticulation** *n.*

reticulocalbin a Ca^{2+}-binding luminal protein of the endoplasmic reticulum. It has six **EF-hands**, a 20-residue N-terminal **signal sequence**, and the *C*-terminal sequence **HDEL**. Example (precursor) from mouse: database code RCA1_MOUSE, 325 amino acids (38.07 kDa).

reticulocyte an immature **erythrocyte** that is capable of protein synthesis, most of the protein synthesized (about 90%) being hemoglobin. It retains intracellular organelles, including mitochondria, and histologically stains for the presence of ribosomes. The name implies misleadingly that it has a **reticulum** (def. 1), which is characteristic of cells that secrete protein, a function not possessed by the reticulocyte.

reticulocyte lysate the preparation obtained by suspending **reticulocytes** in distilled water so that the cells are lysed by osmotic shock. The reticulocytes are usually obtained from rabbits in which **reticulocytosis** has been induced by the administration of phenylhydrazine. The residual RNA is usually removed by the addition of a ribonuclease that is calcium-dependent and is thereby inactivated by the addition of EDTA. Such a lysate is often used for the *in vitro* translation of added mRNA.

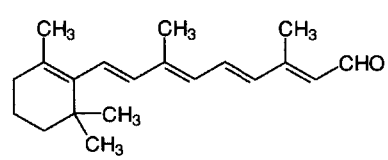
reticulocytosis enhanced levels of reticulocytes in the blood, often due to experimentally-induced increased production. *See also* **reticulocyte lysate**.

reticuloendothelial system *a former name for* **mononuclear phagocyte system**.

reticulum **1** the **endoplasmic reticulum**, a netlike structure of membranes found in the cytoplasm. **2** the most anterior chamber of the ruminant stomach.

retina the light-sensitive layer lining the inside of the posterior wall of the eye in vertebrates and some classes of molluscs. The inner nervous layer of the vertebrate retina is transparent and contains photoreceptive **cone cells** and/or **rod cells** together with their associated nerve cells and fibres, glia, and blood vessels; the outer layer, next to the choroid, is darkly pigmented and prevents back-reflection of light.

retinal **1** pertaining to the retina. **2** *the recommended trivial name for* (2*E*,4*E*,6*E*,8*E*)-3,7-dimethyl-9-(2,6,6-trimethylcyclohex-1-en-1-yl)nona-2,4,6,8-tetraen-1-al; *other names*: $retinal_1$; retinaldehyde; vitamin A aldehyde; vitamin A_1 aldehyde; retinene; $retinene_1$; a compound that plays an important role in the visual process in most vertebrates (*compare* **3,4-didehydroretinal**). In the retina this (all-*E*)-isomer, commonly distinguished as all-*trans*-retinal, is converted by **retinal isomerase** to its (2*E*,4*Z*,6*E*,8*E*)-stereoisomer, generally termed 11-*cis*-retinal, which then combines (as a Schiff's base) with an opsin to form (in cone cells) **iodopsin** or (in rod cells) **rhodopsin**. Interaction with a photon brings about dissociation of iodopsin or rhodopsin, to regenerate all-*trans*-retinal and the opsin, thereby completing the visual cycle. Retinal is formed in the retina by enzymic oxidation of **retinol**; in addition, most vertebrates can convert dietary α-, β-, and γ-carotenes to retinal by oxidative cleavage of the polyprenyl chain at its midpoint. [*Note*: (1) The numbering system of the systematic name is different from that of the trivial name, the latter following the rules used for carotenoids. (2) The fuller name **retinaldehyde** is recommended if confusion with def. 1 may occur.]



all-*trans*-retinal

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retinal$_1$ *(sometimes) an alternative name for* **retinal** (def. 2) (especially to distinguish it from **retinal$_2$**; not recommended).

retinal$_2$ *(sometimes) an alternative name for* **3,4-didehydroretinal** (especially to distinguish it from **retinal$_1$**; not recommended).

retinal cone *see* **cone cell**.

retinaldehyde *see* **retinal**.

retinal isomerase EC 5.2.1.3; *systematic name*: *all-trans*-retinal 11-*cis*-*trans*-isomerase; *other name*: retinene isomerase; an enzyme that catalyses the conversion of all-*trans*-retinal to 11-*cis*-retinal. Example from *Todarodes pacificus* (Japanese flying squid): database code REIS_TODPA, 301 amino acids (33.45 kDa). *See also* **retinal** (def. 2).

retinal rod *see* **rod cell**.

retinene *or* **retinene$_1$** *an alternative name for* **retinal** (def. 2) (not recommended).

retinene$_2$ *an alternative name for* **3,4-didehydroretinal** (not recommended).

retinene isomerase *an alternative name for* **retinal isomerase**.

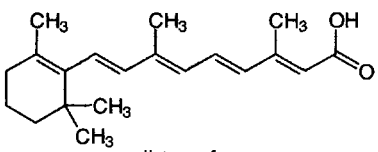
retinitis pigmentosa a relatively common genetic disorder which in humans affects 1 in 4000 people and is caused by the premature death of photoreceptors. The result is progressive night blindness, contraction of the visual field and finally complete loss of sight. One form of autosomal dominant disease results from an abnormality on chromosome 3. In this, there is a single amino-acid substitution in the **rhodopsin** molecule caused by a base transversion of C to A, which results in the change of a proline to a histidine residue at position 23 in the **opsin** molecule, causing the characteristic retinal degeneration. Another severe form of the disease, affecting up to around 20% of some populations, is X-linked; it usually becomes manifest within the first two decades of life and progresses to blindness within 10–20 years. The gene, named *RPGR*, for this form has now been found on the short arm of the X-chromosome. The predicted 90 kDa protein product of the *RPGR* gene bears significant homology to the **RCC1 family**.

retinoate **1** the anion of **retinoic acid**. **2** any salt or ester of retinoic acid.

retinoblastoma a childhood cancer of the developing retina. The offspring of surviving victims have a high incidence of this disease as well as several other types of malignancies. Retinoblastoma is associated with the inheritance of a copy of chromosome-13 from which a particular segment has been deleted. It develops through a mutation in a retinoblast (a retinal precursor cell). The affected chromosomal segment contains the ***RB*** gene which specifies a factor that restrains uninhibited cell proliferation. Thus the *RB* gene is a **tumour suppressor gene**. *See also* **retinoblastoma protein**.

retinoblastoma protein *abbr.*: pRb; the product of the retinoblastoma gene, ***RB***. pRb is a 105 kDa DNA-binding protein that is localized in the nucleus of normal retinal cells but absent in **retinoblastoma** cells. The protein is phosphorylated in the cell cycle by protein kinase **CDC2**. It appears that the interaction of pRb with various **transcription factors** suppresses cellular proliferation. Example: database code RB_HUMAN, 928 amino acids (106.04 kDa).

retinoic acid *the recommended trivial name for* (2*E*,4*E*,6*E*,8*E*)-3,7-dimethyl-9-(2,6,6-trimethylcyclohex-1-en-1-yl)nona-2,4,6,8-tetraenoic acid; *other names*: **tretinoin**; vitamin A acid; vitamin A_1 acid; it is formed from **retinal** by enzymic oxidation in kidney and other tissues, and is active in preventing some, but not all, of the symptoms of vitamin A deficiency. It is a morphogen and regulator of differentiation during embryogenesis. *See also* **retinoic acid receptor**, **vitamin A**.

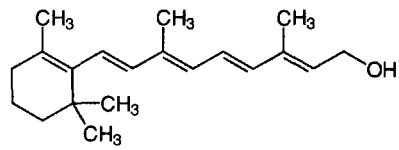


all-*trans* form

retinoic acid receptor a nuclear receptor for **retinoic acid** that mediates its effects on cells. These receptors bind retinoic acid and directly regulate gene expression. The proteins belong to the steroid/thyroid/retinoic acid family of nuclear receptors for hormones. The ligand-binding domain is in the C-terminal region, the zinc-finger DNA-binding domain in a central region, and a function-modulating domain in the N-terminal region. Binding of hormone induces changes in receptor conformation that control transcriptional activation and repression, and also regulates homo- or heterodimerization. In the absence of ligand, these receptors repress basal gene expression, probably through co-repressor proteins. α, β, γ and δ types of receptor are known. Example, α-1 receptor from *Mus musculus*: database code RRA1_MOUSE, 462 amino acids (50.73 kDa).

retinoid any member of a class of isoprenoids, whether naturally occurring or not, that contain or are derived from four prenyl groups linked in a head-to-tail manner. All retinoids may formally be derived from a monocyclic parent compound with 20 carbon atoms containing five carbon–carbon double bonds and a functional group at the terminus of its acyclic moiety.

retinol *the recommended trivial name and international nonproprietary name for* (2*E*,4*E*,6*E*,8*E*)-3,7-dimethyl-9-(2,6,6-trimethylcyclohex-1-en-1-yl)nona-2,4,6,8-tetraen-1-ol; *other names*: retinol$_1$; vitamin A; vitamin A_1; vitamin A alcohol; vitamin A_1 alcohol; axerophthol; axerol; the predominant form of **vitamin A** in higher vertebrates and marine fishes (*compare* **3,4-didehydroretinol**). It is stored primarily in the liver, almost entirely as the ester, retinyl palmitate.



all-*trans* form

retinoyl the acyl group formally derived from **retinoic acid**.

retinyl the alkyl group formally derived from **retinol** by loss of its hydroxyl group.

retro- *prefix* signifying backwards, or in the reverse direction.

retroendocytosis the process by which some particles, e.g. low-density lipoproteins, are released, after receptor-binding and endocytosis, back into the medium rather than being degraded within lysosomes.

retrogene a segment of DNA that has arisen by reverse transcription of the genetic material in an RNA virus (**retrovirus**) and incorporation of the DNA so formed into the host cell's genomic DNA.

retrogradation the spontaneous irreversible change of a liquid colloidal solution to an insoluble or gelled state. The term is used especially of aqueous amylose solutions in which microcrystalline precipitates of aligned, hydrogen-bonded amylose molecules occur on standing.

retrograde **1** moving backwards; reverse or inverse; tending towards a former state or condition; deteriorating. **2** to move backwards or in reverse, as in retrograde transport.

retrogress to move backwards or in a less favourable direction; to deteriorate or degenerate. —**retrogression** *n.*; **retrogressive** *adj.*

retroinhibition *an alternative name for* **feedback inhibition**.

retropepsin EC 3.4.23.16; a **pepsin**-type endopeptidase from **HIV** that catalyses the hydrolysis of Xaa-|-Xbb bonds, where Xaa is a hydrophobic residue, and Xbb is variable, but often is Pro. It is part of the polyprotein product of the ***pol*** gene. This polyprotein also contains reverse transcriptase and ribonucle-

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ase H. Example from HIV-1: database code NRL_1HHP, 99 amino acids (10.78 kDa); 3-D structure known.

retroposon *or* **retrotransposon** a **transposable element** that uses a mechanism indistinguishable from part of a retroviral life cycle. Retroposons are present in a wide variety of organisms, such as yeast, *Drosophila*, and mammals. A good example is the Ty1 element of yeast: after the formation of a double-stranded DNA by **reverse transcriptase** it is integrated into a random site on the chromosome.

retroregulation the regulation of translation of messenger RNA (mRNA) by a sequence that is downstream of the region undergoing translation. For example, an mRNA of phage lambda carrying the sequence of gene *int* is not normally translated; mutation in a site called *sib*, located downstream of the *int* coding sequence, allows translation of the *int* mRNA.

retrotransposon *an alternative name for* **retroposon**.

Retrovir *see* **zidovudine**.

retroviral oncogene *see* **oncogene, retrovirus**.

retrovirus *or* **ribodeoxyvirus** *or* **RNA–DNA virus** any virus belonging to the family Retroviridae. This comprises single-stranded RNA animal viruses characterized by two unique features: firstly, their genome is diploid, consisting of two copies of the RNA; secondly, this RNA is transcribed by the virion-associated enzyme **reverse transcriptase** into double-stranded DNA. This double-stranded DNA, or **provirus**, can then integrate into the host genome and be passed from parent cell to progeny cell as a stably integrated component of the host genome. The virion is an enveloped, roundish particle, ≈100 nm in diameter, with a helical nucleocapsid containing 6 MDa of RNA, consisting of two identical molecules of ≈3 MDa each, joined to their 5′ ends and hydrogen-bonded into loops (70S RNA), plus small (45S) RNA from the host. The genome is bounded at each end by long terminal repeat sequences and comprises at least three genes: *gag*, which encodes for the inner capsid protein; *pol*, which codes for a polyprotein containing **retropepsin**, ribonuclease H (*see* **ribonuclease**), and **reverse transcriptase**; and *env*, which codes for the spikes on the envelope. Members of a subfamily of retroviruses, known as the Oncovirinae (or the RNA tumour viruses), contain an additional **oncogene**, which confers on the virus the ability to form tumours in the host. These oncoviruses include the Rous sarcoma virus and other leukosis viruses of birds, and a number of viruses causing leukemia in various mammals (not in humans). Tumour-producing retroviruses have also been called **oncornaviruses**, **rousviruses**, and **leukoviruses**. Other subfamilies include the Spumavirinae (spumaviruses) and the Lentivirinae (lentiviruses); **HIV** is a member of the latter. The retroviruses are in class VI of the **Baltimore classification**.

reverse dialysis a technique for the concentration of macromolecules in solution. The (dilute) solution is placed in a bag made of a semipermeable material, through which the macromolecules cannot pass but water and other small molecules can. The bag is placed in a bed of dry water-soluble polymer (which cannot enter the membrane) such as polyethylene glycol. Water, together with other small molecules, is then drawn out of the bag into the external phase until equilibrium is reached, thereby concentrating the solution of macromolecules in the bag. *Compare* **dialysis**.

reversed phase *or* **reverse phase** a system used in **adsorption chromatography** (often thin-layer or high-pressure liquid chromatography), in which the **stationary phase** consists of a material with a hydrophobic surface. In such a system, molecules migrate in order of polarity, the most polar migrating fastest. In column chromatography, mobile phases are used in a sequence commencing with more polar solvents and proceeding in decreasing order of polarity, the reverse of the sequence used in normal phase chromatography. The stationary phase often consists of silicic acid in which all hydrophilic groups are masked by silanization.

reversed rocket immunoelectrophoresis a variant of **rocket immunoelectrophoresis** in which antibodies are forced by electrophoresis through antigen-containing agarose gel, the heights of the 'rockets' so formed being related to the antibody concentrations. It is useful for titre determinations in large series of antibody samples.

reverse genetics *another name for* **positional cloning** *a term coined to describe* the study of the biological consequences to an organism of artificial alteration of its DNA. The changes may be either gross (e.g. deletion, insertion, or transposition of segments of DNA effected by recombinant DNA technology) or limited to specific loci (e.g. base substitution through site-directed mutagenesis).

reverse gyrase an ATPase enzyme with a **DNA helicase**-like domain and a type-I **(DNA) topoisomerase** in the same protein. It is able to induce positive supercoiling into DNA, a property of DNA that is found only in bacteria that express this enzyme. Example (deduced from DNA sequence) from *Sulfolobus acidocaldarius* (an archaebacterium): database code SSOREVGYRA, 780 amino acids (87.38 kDa).

reverse mutation a heritable change in a mutant gene that restores a nucleotide sequence to that which obtained prior to mutation. *Compare* **back mutation, reversion**.

reverse osmosis the pressure-induced flow of solvent through a semipermeable membrane in a direction that enhances any existing difference in the activities (or concentrations) of the nonpermeant solutes on the two sides of the membrane (*compare* **osmosis**). The principle can be used in the preparation of purified water from tap water or sea water.

reverse phase *see* **reversed phase**.

reverse pinocytosis *see* **exocytosis**.

reverse transcriptase EC 2.7.7.49; *recommended name*: RNA-directed DNA polymerase; *systematic name*: deoxynucleoside-triphosphate: DNA deoxynucleotidyltransferase (RNA-directed); *other names*: DNA nucleotidyltransferase (RNA-directed); revertase. A DNA polymerase enzyme, found particularly in retroviruses and possibly in normal animal cells, that uses either DNA or RNA as a template. It catalyses a reaction between a deoxynucleoside triphosphate and DNA_n to form pyrophosphate and DNA_{n+1}; this protein also has **ribonuclease H** (RNase H) activity. When the single-stranded RNA of the retrovirus enters a cell, the enzyme first makes a DNA copy of one of the **long terminal repeats** of the viral genomic RNA strand using a tRNA as a primer. The stretch of RNA used as a template is then digested by the RNase H activity of the enzyme, releasing the newly synthesized stretch of DNA which then pairs with a complementary stretch of viral RNA to form a DNA–RNA hybrid. This is then used by the same enzyme to make a double-stranded DNA which circularizes and integrates into a host cell chromosome. Examples: (i) AZT-resistant variant of HIV enzyme, database code A47175, 559 amino acids (64.32 kDa); 3-D structures known for parts of the HIV enzyme (database codes NRL_1HRHA2, NRL_1HRHB2); (ii) from *Escherichia coli* retron EC67: database code RT67_ECOLI, 586 amino acids (67.16 kDa). Reverse transcriptase lacks a proof-reading exonuclease function and is highly error-prone. It can thus evolve even within a single patient, and this interferes with long-term therapy. Reverse transcriptase is used in cDNA technology to make cDNA from RNA. **Telomerase** is a template-bearing reverse transcriptase.

reverse transcription the process carried out by **reverse transcriptase**. *See also* **transcription**.

reverse turn *(in protein structure)* a structural feature that allows the peptide chain to turn back through about 180° by what is termed a **beta bend**.

reversible competitive antagonist *(in pharmacology)* an antagonist for which the rate of dissociation from its receptor is relatively high, such that by increasing the concentration of an agonist the receptor **occupancy** (def. 2) of the antagonist falls. At sufficiently high concentrations of agonist a maximal tissue response can be obtained, even in the presence of the an-

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tagonist, such that the extent of antagonism is determined by the relative concentrations of agonist and antagonist.

reversible inhibition (of an enzyme or other system) a type of inhibition that occurs when the equilibrium between free inhibitor and the inhibitor–enzyme (or system) complex lies sufficiently far towards the free inhibitor state for the inhibitor to be readily removed, leaving an active enzyme (or system).

reversible reaction a reaction in which the **equilibrium constant** is such that the reaction can be made to proceed at a detectable rate in either direction under appropriate conditions.

reversion the restoration, by a second mutation, of the genomic base sequence of a mutant virus or organism to that of the parental strain. Less strictly, any return to the original **phenotype**. *See also* **back mutation**, **reverse mutation**.

reversion frequency the proportion of the total number of cells in a population that undergo **reversion**.

reversion spectroscope a **spectroscope** in which two spectra alongside each other, one of which is reversed by optical means, are formed by the entering light. The two spectra may be moved longitudinally relative to each other by moving a micrometer screw. If two absorption bands are aligned when a particular substance, e.g. oxyhemoglobin, is viewed, the amount by which the screw has to be turned to align the same band when a mixture of the same substance and another with a similar absorption spectrum, e.g. carbonmonoxyhemoglobin, is viewed is related to the proportion of the second substance present.

revertant **1** a mutant that has partially or completely regained the wild-type phenotype. **2** a gene that has undergone **reversion**.

revertase *an alternative name for* **reverse transcriptase**.

Reynolds number *symbol*: *Re*; a nondimensional parameter of fluid motion through a cylindrical tube or past an obstruction. It is given by the expression vl/ν, where l has the dimensions of length, v is the fluid's velocity, and ν is the kinematic viscosity. In general, low Reynolds numbers show that viscous forces predominate in controlling the flow, while high Reynolds numbers indicate that inertial forces are more important. [After Osborne Reynolds (1842–1912), Irish physicist and engineer.]

RF *abbr. for* **1** release factor. **2** replicative form.

R factor **1** *abbr. for* resistance factor (i.e. **resistance plasmid**). **2** *(formerly) abbr. for* release factor.

rfDNA *see* **DNA**.

RFLP *abbr. for* restriction fragment length polymorphism.

R form **1** *abbr. for* relaxed form (of a protein). **2** **R-form** (hyphenated) *abbr. for* rough form; describing bacterial colonies with a jagged perimeter.

RGD the amino-acid sequence Arg–Gly–Asp, which is present in **fibronectin** and some other extracellular matrix proteins and is recognized by some **integrins** that bind these proteins.

RGK-2 *see* **tonin**.

rH the negative logarithm of the concentration (expressed as pressure in atmospheres) of hydrogen gas in equilibrium with a redox system; i.e.

$$\mathrm{rH} = -\log[\mathrm{H_2}].$$

Also,

$$\mathrm{rH} = 2(E_h F)/(RT\ln 10) + \mathrm{pH},$$

where F is the Faraday constant, R the gas constant, T the thermodynamic temperature, and E_h the **redox potential** at the pH of the system under study.

Rh **1** *abbr. for* Rhesus factor. **2** *symbol for* rhodium.

Rha *symbol for* rhamnose.

Rhabdoviridae a family of single-stranded RNA viruses infecting vertebrates, arthropods, amoebae, and plants, whose members are identified by their elongated rod or bullet-shaped appearance. The virions are 70–80 nm particles, covered with a lipid envelope. They contain negative-strand RNA together with RNA-dependent RNA polymerase, which transcribes the genome directly to mRNA – they are class IV viruses in the **Baltimore classification**. Rhabdoviruses are usually transmitted by arthropods; they include the plant rhabdoviruses, the vesiculoviruses (e.g. the vesicular stomatitis virus of cattle), the lyssaviruses, which include the rabies virus, and sigma virus of *Drosophila*. [From Greek *rhabdos*, rod.]

rhabdovirus *see* **Rhabdoviridae**.

L-rhamnosamine 2-amino-2,6-dideoxy-L-mannose; an amino sugar that occurs in some bacterial lipopolysaccharides.

rhamnose *symbol*: Rha; 6-deoxy-L-mannose; a monosaccharide (hexose) that occurs commonly as a compound of plant glycosides, in polysaccharides of gums and mucilages, and in bacterial polysaccharides; it is also a component of some plant cell-wall polysaccharides, and frequently acts as the sugar component of flavonoids. Free rhamnose is also found in some plants. The D-enantiomer occurs in some bacterial capsular polysaccharides. *See also* **L-rhamnose isomerase**.

L-rhamnose isomerase EC 5.3.1.14; *systematic name*: L-rhamnose ketol-isomerase; an enzyme that catalyses the interconversion of L-rhamnose and L-rhamnulose. It initiates the catabolism of rhamnose. L-rhamnulose is then phosphorylated by rhamnulose kinase, EC 2.7.1.5, to L-rhamnulose-1-phosphate which is cleaved by rhamnulose-1-phosphate aldolase, EC 4.1.2.19, to glycerone phosphate and (*S*)-lactaldehyde. Example from *Escherichia coli*: database code RHAA_ECOLI, 419 amino acids (47.12 kDa).

rhamnulose 6-deoxyfructose; its formation by **L-rhamnose isomerase** initiates rhamnose catabolism.

rheology the science concerning the deformation and flow of matter. —**rheological** *adj.*

rheoseme *or* **flow signal** a chemical messenger or transmitter substance (other than a neurotransmitter) carried from a site of generation to site of action within a cell (e.g. a neuron) by cytoplasmic flow; a translocated **bioseme** or **second messenger**.

rheostat a device in which a controllable resistance is introduced into an electrical circuit to vary the output to permit an apparatus to be regulated within desired limits.

Rhesus factor *abbr.*: Rh; a protein associated with the rhesus (Rh) system of blood groups in humans. The system was so designated as a result of the finding that rabbit and guinea-pig antibodies raised against erythrocytes from *Macacus rhesus* monkeys agglutinated erythrocytes from 85% of the random human population. Initially an antigen, designated D, was isolated from the erythrocytes of Rh-positive individuals; those lacking D were classified Rh-negative. Subsequently, another antigen, LW (Landsteiner-Weiner), was identified, which, although phenotypically similar to D, is encoded by a gene that segregates independently from *Rh*. C and E antigens have also been found. The antigenic determinant is associated with the protein structure. In hemolytic disease of the newborn due to rhesus incompatibility, antibodies from a Rh-negative mother, often formed during the birth of a previous Rh-positive child whose blood has entered the mother's bloodstream, pass across the placenta and cause destruction of fetal red cells.

rhinovirus any of a group of small RNA viruses belonging to the Picornaviridae family, members of which are responsible for the common cold in humans, and foot-and-mouth disease in cattle.

Rhizobium a genus of soil bacteria whose members reside in specialized root nodules of leguminous plants and set up a symbiosis. The bacteria are active in **nitrogen fixation** providing the plant with organic nitrogen and obtaining carbon compounds in return. Many if not all *Rhizobium* species contain plasmids, which enable them to colonize their host plant species.

rhizomorph a stout, rootlike mass of hyphae, produced by some fungi, that serves to generate vegetative spread.

rho *symbol*: ρ (lower case) *or* P (upper case); the seventeenth letter of the Greek alphabet. For uses *see* **Appendix A**. *See also* **rho protein**, **Rho protein**.

Rhodamine any of a series of dyes based on 9-(2-carboxyphenyl)xanthine. Rhodamine 6G, *N*-[9-(2-carboxyethylphenyl)-

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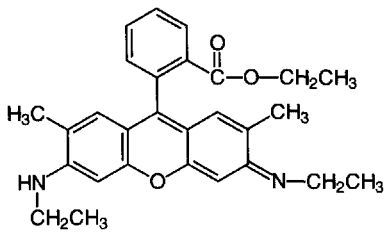
6-(diethylamino)-3*H*-xanthen-3-ylidene]ethylethanamine, is used as a spray to reveal lipids as pink fluorescent spots after thin-layer chromatography.



Rhodamine 6G

rhodanese EC 2.8.1.1; *recommended name*: thiosulfate sulfurtransferase; *systematic name*: thiosulfate:cyanide sulfur-transferase; *other names*: thiosulfate cyanide transsulfurase; thiosulfate thiotransferase. An enzyme that catalyses the displacement of sulfite from thiosulfate by cyanide ion, forming sulfite and thiocyanate and thus detoxifying cyanide. It is of interest structurally in having two domains of closely similar conformation yet very different sequence. Example from *Gallus gallus* (chicken): database code THTR_CHICK, 289 amino acids (32.25 kDa). [From the use of rhodanate as a name for thiocyanate.]

rhodanid any of a group of **thiocyanates** produced by the metabolism of mustard-oil glycosides (glycosinolates) in damaged leaf tissues.

rhodium *symbol*: Rh; a silvery-white metallic transition element of group VIII of the (IUPAC) **periodic table**; atomic number 45; relative atomic mass 102.9. It occurs mainly in oxidation state III. A rare member of the platinum metals, it possesses marked properties of nobility, being, e.g., resistant to nitric acid and aqua regia.

rhodo+ *or (before a vowel)* **rhod+** *comb. form* indicating a red colour, or the odour of a rose. [From Greek *rhodos*, rose.]

rhodopsin *or* **visual purple** a brilliant purplish-red, light-sensitive visual pigment found in the rod cells of the retinas of most vertebrates (exceptions being freshwater and migratory fish and some amphibians). It is a seven-transmembrane-domain protein homologous to other members of the G-protein-linked receptor family. It consists of a rod-type **opsin** combined (as a Schiff's base) with 11-*cis*-retinal (*see* **retinal**). It has an absorption maximum at ≈500 nm. *Compare* **porphyropsin**. A single amino-acid substitution in the rhodopsin molecule causes one form of **retinitis pigmentosa** in humans. *See also* **bacteriorhodopsin**, **halorhodopsin**, **slow-cycling rhodopsin**.

rho factor *an alternative name for* **rho protein**.

rho protein *or (sometimes)* **rho factor** a bacterial protein, an ATP-dependent helicase, that facilitates transcription termination. Binding of rho to the nascent RNA is followed by activation of rho's RNA-dependent ATPase activity, and release of the mRNA from the DNA template; it recognizes and binds to C-rich regions of the RNA transcript. In *Escherichia coli* this protein is the site of action of the antibiotic bicyclomycin, which binds to rho protein and inhibits its ATPase activity. Example from *E. coli*: database code RHO_ECOLI, 419 amino acids (46.95 kDa). *Compare* **Rho protein**.

Rho protein a small Ras-related GTPase (*see* ***RAS***), involved in controlling the polymerization of actin into filaments, and subsequent organization. *RHOB* is an early response gene transiently induced in fibroblasts by platelet-derived growth factor or epidermal growth factor; its overexpression can be tumorigenic. *Compare* **rho protein**.

RI *abbr. for* refractive index.

RIA *abbr. for* radioimmunoassay.

Rib *symbol for* ribose.

ribaric acid one of the **pentaric acids**. *See also* **aldaric acid**.

ribitol *or (formerly)* **adonitol** a **pentitol** derived formally by reduction of the –CHO group of either D- or L-ribose. It is a *meso* compound and does not require a D or L configurational descriptor. It occurs free in some plants and is a component of **riboflavin**.

ribitol teichoic acid a complex polymer of **ribitol** residues linked by phosphate groups, substituted by glucosyl or acetylglucosamine residues and ester-linked to D-alanine. It is found in the walls of Gram-positive bacteria.

ribo+ *comb. form* **1** of, relating to, or containing **ribose**, especially as opposed to deoxyribose. **2** containing a ribose residue linked through its anomeric carbon. It is used also in **riboflavin**, inappropriately, for a ribitol residue.

ribo- *prefix (in chemical nomenclature)* indicating a particular configuration of three contiguous >CHOH groups (as found in the acyclic form of D- or L-ribose). *See also* **monosaccharide**.

ribocharin an acidic protein specifically associated with the granular component of the nucleolus and nucleoplasmic 65S particles. These particles contain the nuclear 28S rRNA and may represent the precursor to the large ribosomal subunit.

ribodeoxyvirus *(sometimes)* any RNA virus that replicates via DNA; such viruses are now usually known as **retroviruses**. *Compare* **deoxyribovirus**.

riboflavin *an alternative name for* **vitamin B_2**.

ribofuranosyl *an alternative term for* **ribosyl**.

ribonuclease *abbr.*: RNase *or (sometimes)* RNAase; any of a group of nuclease enzymes that cleave phosphodiester bonds in chains of RNA. With the exception of RNase P, which is a **ribozyme**, they are all proteins. As in the case of other enzymes that hydrolyse macromolecules, RNAses are classified according to whether they are **exoribonucleases**, catalysing sequential cleavage of mononucleotides from either a free 5′ or 3′ terminus, or both, or **endonucleases**, cleaving bonds within the polyribonucleotide chain. Endonucleases, which unlike exonucleases can cleave circular molecules of RNA, fall into further categories according to whether they cleave only specific sites or at any phosphodiester linkage. Enzymes that cleave RNA fall into eight subclasses: EC 3.1.13, exoribonucleases producing 5′-phosphomonoesters; EC 3.1.14, exoribonucleases producing other than 5′-phosphomonoesters; EC 3.1.15, exonucleases active with either ribo- or deoxyribonucleic acids and producing 5′-phosphomonoesters; EC 3.1.16, exonucleases active with either ribo- or deoxyribonucleic acids and producing other than 5′-phosphomonoesters; EC 3.1.26, endoribonucleases producing 5′-phosphomonoesters; EC 3.1.27, endoribonucleases producing other than 5′-phosphomonoesters; EC 3.1.30, endonucleases active with either ribo- or deoxyribonucleic acids and producing 5′-phosphomonoesters; and EC 3.1.31, endonucleases active with either ribo- or deoxyribonucleic acids and producing other than 5′-phosphomonoesters. Ribonucleases include enzymes having mechanisms of (A) phosphotransferases, (B) phosphodiesterases, or (C) phosphorylases. In group C are polynucleotide phosphorylase and polynucleotide pyrophosphorylase. The differences between groups A and B are more than pedantic. Thus the feature of group A is the involvement of the 2′-OH group in an intramolecular attack at the adjacent phosphodiester bond, in addition to a property for conferring specificity for one or more of the four bases. The nucleoside 2′:3′-cyclic phosphates are obligate intermediate products. In group B, a direct attack of water on the 3′:5′-phosphodiester bond is catalysed. This latter group includes, therefore, the enzymes that hydrolyse both RNA and DNA and those that cleave diester bridges in RNA to form only 5′-nucleotide products. Thus group A enzymes may be classed as cyclizing and group B enzymes as non-cyclizing. The group A enzymes do not depend for their activity on divalent cations whereas the group B enzymes require Mg^{2+} or Ca^{2+}. Within each group of enzymes there are many types, as described below.

Exoribonucleases catalyse the sequential cleavage of mono-

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nucleotides from one or other, or both, ends of the polynucleotide. **Exoribonuclease II** EC 3.1.13.1; *other name*: ribonuclease II; reaction: exonucleolytic cleavage in the 3′- to 5′-direction to yield 5′-phosphomononucleotides. **Exoribonuclease H** EC 3.1.13.2; reaction: exonucleolytic cleavage to 5′-phosphomonoester oligonucleotides in both 5′- to 3′- and 3′- to 5′-directions. Example from *E. coli*: database code RNB_ECOLI, 644 amino acids (72.4 kDa). **Poly(A)-specific ribonuclease** EC 3.1.13.4; reaction: exonucleolytic cleavage of poly(A) to 5′-AMP. **Yeast ribonuclease** EC 3.1.14.1; reaction: exonucleolytic cleavage to 3′-phosphomononucleotides.

Endoribonucleases cleave the polynucleotide internally. This first group (sub-subclass EC 3.1.26) produce exclusively 5′-phosphomonoesters. ***Physarum polycephalum* ribonuclease** EC 3.1.26.1; reaction: endonucleolytic cleavage to 5′-phosphomonoester. **Ribonuclease alpha** EC 3.1.26.2; reaction: endonucleolytic cleavage to 5′-phosphomonoester. **Ribonuclease III** EC 3.1.26.3; *other names:* RNase O; RNase D; reaction: endonucleolytic cleavage to 5′-phosphomonoester. Example from *Rhodobacter capsulatus*: database code RCLEPRNCG, 265 amino acids (28.8 kDa). **Ribonuclease H** EC 3.1.26.4; *other names:* endoribonuclease H (calf thymus); calf thymus ribonuclease H; reaction: endonucleolytic cleavage to 5′-phosphomonoester; required for removing RNA from **Okazaki fragments**; *see also* **RNA-directed DNA polymerase**. **Ribonuclease P** EC 3.1.26.5; reaction: endonucleolytic cleavage of RNA, removing 5′-sequence of extra nucleotides from tRNA precursor; it is a **ribozyme**; *see* **RNase P**. **Ribonuclease IV** EC 3.1.26.6; *other names:* endoribonuclease IV; poly(A)-specific ribonuclease; reaction: endonucleolytic cleavage of poly(A) to fragments terminated by 3′-hydroxyl and 5′-phosphate groups. Example from yeast: PAN1_YEAST, 1480 amino acids (160 kDa). **Ribonuclease P4** EC 3.1.26.7; reaction: endonucleolytic cleavage of RNA, removing 3′-sequence of extra nucleotides from tRNA precursor. **Ribonuclease M5** EC 3.1.26.8; *other name:* 5S rRNA maturation nuclease; reaction: endonucleolytic cleavage of RNA, removing 21 and 42 nucleotides, respectively, from the 5′- and 3′-termini of a 5S rRNA precursor. **Ribonuclease (poly(U)-specific)** EC 3.1.26.9; reaction: endonucleolytic cleavage of poly(U) to fragments terminated by 3′-hydroxyl and 5′-phosphate groups. **Ribonuclease IX** EC 3.1.26.10; reaction: endonucleolytic cleavage of poly(U) or poly(C) to fragments terminated by 3′-hydroxyl and 5′-phosphate groups.

The second group of endoribonucleases (sub-subclass EC 3.1.27) yield products other than 5′-phosphomonoesters. **Ribonuclease T2** EC 3.1.27.1; *other name:* ribonuclease II; reaction: two-stage endonucleolytic cleavage to 3′-phosphomononucleotides and 3′-phosphooligonucleotides with 2′,3′-cyclic phosphate intermediates. Example (glycoprotein precursor) from *Aspergillus oryzae*: database code RTN2_ASPOR, 276 amino acids (30.71 kDa); residues 1–17 are the signal. ***Bacillus subtilis* ribonuclease** EC 3.1.27.2; reaction: endonucleolytic cleavage to 2′,3′-cyclic nucleotides. **Ribonuclease T1** EC 3.1.27.3; *other names:* guanyloribonuclease; *Aspergillus oryzae* ribonuclease; ribonuclease N1; ribonuclease N2; reaction: two-stage endonucleolytic cleavage to 3′-phosphomononucleotides and 3′-phosphooligonucleotides ending in G-p with 2′,3′-cyclic phosphate intermediates. Database code NRL_5RNT, 104 amino acids (11.08 kDa); 3-D structure known, including bound intermediate. **Ribonuclease U2** EC 3.1.27.4; reaction: two-stage endonucleolytic cleavage to 3′-phosphomononucleotides and 3′-phosphooligonucleotides ending in Ap or Gp with 2′,3′-cyclic phosphate intermediates. Example from the smut fungus, *Ustilago sphaerogena*: database code RNU2_USTSP, 113 amino acids (12.26 kDa). **Pancreatic ribonuclease** EC 3.1.27.5; *other names:* ribonuclease; ribonuclease I; ribonuclease A; reaction: endonucleolytic cleavage to 3′-phosphomononucleotides and 3′-phosphooligonucleotides ending in Cp or Up with 2′,3′-cyclic phosphate intermediates. Example (bovine): database code NRL_3RN3, 124 amino acids (13.68 kDa); 3-D structure known. ***Enterobacter* ribonuclease** EC 3.1.27.6; reaction: endonucleolytic cleavage to 3′-phosphomononucleotides and 3′-phosphooligonucleotides with 2′,3′-cyclic phosphate intermediates. Example (precursor) from *E. coli*: database code RNI_ECOLI, 268 amino acids (29.58 kDa); residues 1–23 are the signal sequence. **Ribonuclease F** EC 3.1.27.7; reaction: endonucleolytic cleavage of RNA precursor into two, leaving 5′-hydroxyl and 3′-phosphate groups. **Ribonuclease V** EC 3.1.27.8; *other name:* endoribonuclease V; reaction: hydrolysis of poly(A), forming oligoribonucleotides and ultimately 3′-AMP. *Compare* **deoxyribonuclease**.

ribonucleate **1** *abbr.*: RNA; any anionic form of ribonucleic acid. **2** any salt of ribonucleic acid.

ribonucleic acid *abbr.*: RNA; *former names*: pentose nucleic acid (*abbr.*: PNA); ribose nucleic acid; yeast nucleic acid. *See* **RNA**.

ribonucleoprotein *abbr.*: RNP; any conjugated protein that contains RNA as the nonprotein moiety. Various specific kinds of RNP are listed with their abbreviations at **RNP**.

ribonucleoside any **nucleoside** (def. 1) in which the glycose moiety is β-D-ribofuranose. The link is from C-1 of ribose to N-9 of a purine or to N-1 of a pyrimidine. To distinguish between the numbering systems of the base and sugar, the numbers of the sugar atoms are characterized by the addition of 'prime', i.e. 1′ to 5′. The various products have trivial names, e.g. adenosine, guanosine, cytidine, and uridine. Strictly, the term ribonucleoside should be confined to structures occurring in nucleic acids, but it can be used for any base–ribose compound. By extension, it can be applied to **pseudouridine** (which occurs in tRNA) with a C–C link between ribose and uracil.

ribonucleoside-diphosphate reductase *the recommended name for* **nucleoside-diphosphate reductase**.

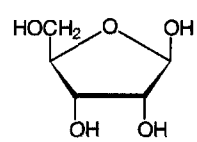
ribonucleoside-triphosphate reductase *the recommended name for* **nucleoside-triphosphate reductase**.

ribonucleotide any ribonucleoside in ester linkage to phosphate, commonly at the 5′ position of the ribose moiety, although some 2′- and 3′-esters and some (cyclic) 2′,3′-, or 3′,5′-diesters are known. The 5′-ribonucleotides are metabolically important; they may be esters of [mono]phosphate, diphosphate, or triphosphate, e.g. guanosine 5′-[mono]phosphate, cytidine 5′-diphosphate, adenosine 5′-triphosphate. *See* **nucleotide**.

ribonucleotide reductase any enzyme that catalyses the reduction of ribonucleotides to deoxyribonucleotides during biosynthesis. *See* **nucleoside-diphosphate reductase**, **nucleoside-triphosphate reductase**.

ribophorin either of two types of protein, ribophorins I and II, that form two essential subunits of ***N*-oligosaccharyltransferase**. They were originally isolated as ribosome-binding proteins of rough endoplasmic reticulum. Examples from human; ribophorin I: database code RIB1_HUMAN, 607 amino acids (68.57 kDa); ribophorin II: database code RIB2_HUMAN, 631 amino acids (69.30 kDa).

ribose *symbol*: Rib; *ribo*-pentose. The D enantiomer, as β-D-ribofuranose, forms the glycose moiety of all ribonucleosides, ribonucleotides, and ribonucleic acids, and also of ribose phosphates, various glycosides, some coenzymes, and some forms of vitamin B_{12}.



β-D-ribofuranose

ribose nucleic acid *a former name for* **ribonucleic acid**.

ribose-5-phosphate epimerase EC 5.3.1.6; *systematic name*: D-ribose-5-phosphate ketol-isomerase; *other names*: phospho-

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pentoisomerase; phosphoriboisomerase. An enzyme that catalyses the reaction:

D-ribose 5-phosphate = D-ribulose 5-phosphate.

It is an enzyme of pentose metabolism, especially the **pentose phosphate pathway**. Example from *Escherichia coli*: database code RPIA_ECOLI, 219 amino acids (22.83 kDa).

ribose-phosphate pyrophosphokinase EC 2.7.6.1; *other name*: phosphoribosyl pyrophosphate synthetase (*abbr.*: PRS); an enzyme that catalyses the formation of 5-phospho-α-D-ribose-1-diphosphate (*abbr.*: PRPP; *other name*: phosphoribosyl pyrophosphate) from ATP and D-ribose 5-phosphate with release of AMP; it is Mg^{2+}-dependent. PRPP is an intermediate in the biosynthesis of histidine and tryptophan, and in the *de novo* biosynthesis of purines and pyrimidines. The enzyme has a well-conserved sequence. Examples: in human there are two isoforms: PRS-II (also in rat): database code KPR1_HUMAN, 317 amino acids (34.66 kDa); PRS-II: database code KPR2_HUMAN, 317 amino acids (34.60 kDa).

riboside the product of the formation of a glycosidic bond between ribose and another group, either through the nitrogen of an amine or a hydroxyl group, i.e. via *N*- or *O*-glycosidic linkages. *See also* **pseudouridine**. *Compare* **ribonucleoside**.

ribosomal DNA *abbr.*: rDNA; the DNA of the genes coding for ribosomal RNA (*see* **ribosome**).

ribosomal protein *abbr.*: r-protein; any of the protein components of the ribosomal subunits. They are typically small, and some are basic. Ribosomal proteins are referred to as S (small subunit) proteins and L (large subunit) proteins; in *Escherichia coli* there are 21 S proteins, designated S1–S21, and 34 L proteins, designated L1–L34. In eukaryotes (e.g. rat liver) there are 33 S proteins and 49 L proteins. *See also* **ribosome**.

ribosomal RNA *abbr.*: rRNA; *see* **ribosome**.

ribosome an intracellular organelle, about 200 Å in diameter, consisting of RNA and protein. It is the site of protein biosynthesis resulting from translation of messenger RNA (mRNA). It consists of two subunits, one large and one small, each containing only protein and RNA. Both the ribosome and its subunits are characterized by their sedimentation coefficients, expressed in **Svedberg units** (*symbol*: S). Hence, the prokaryotic ribosome (70S) comprises a large (50S) subunit and a small (30S) subunit, while the eukaryotic ribosome (80S) comprises a large (60S) subunit and a small (40S) subunit. Several ribosomes may bind to one mRNA to form a **polysome**. Two sites on the ribosomal large subunit are involved in translation, namely the **aminoacyl site** (A site) and **peptidyl site** (P site). Ribosomes from prokaryotes, eukaryotes, mitochondria, and chloroplasts have characteristically distinct **ribosomal proteins**. Prokaryotic ribosomes contain 35–45% protein, while eukaryotic ribosomes contain 50% protein. **Ribosomal RNA** (rRNA) is RNA that forms part of the ribosomal structure. In prokaryotes, a 30S ribosomal subunit contains one 16S RNA molecule with associated proteins, while a 50S subunit contains one 5S and one 23S RNA molecule. In eukaryotes, the 60S subunit contains one 28S, one 5.8S, and one 5S RNA molecule, while the 40S subunit contains one 18S RNA molecule. The structures are known. In *Escherichia coli*, the rRNAs are synthesized as part of a large transcript containing transfer RNA (tRNA) molecules, which is then cleaved during processing. In eukaryotes, the genes for the 5.8S, 18S, and 28S molecules reside in the **nucleolus**, and code for a 40S transcript, which is then cleaved during processing; this includes splicing that occurs in the absence of protein. The gene for the 5S rRNA is a separate transcription unit outside the nucleolus. *See also* **mRNA binding site**, **protein biosynthesis**.

ribosome-inactivating protein *abbr.*: RIP; any of a group of proteins, obtained from plants, that inactivate eukaryotic ribosomes. They are of two types. Type I proteins have a single chain, and include agrostin, dianthrin, dodecandrin, **gelonin**, luffin, momordin, saporin, and tritin. They are enzymes, EC 3.2.2.22, that catalyse endohydrolysis of the N-glycosyl bond at one specific adenosine on 28S rRNA. They are plant protein toxins and possibly have antiviral activity. Examples: **luffin**, from the smooth loofah, *Luffa cylindrica*, has two subunits; precursor sequences: database code RIPA_LUFCY, 277 amino acids (30.18 kDa), and database code RIPB_LUFCY, 250 amino acids (27.26 kDa); **saporin-2** from *Saponaria officinalis*: database code RIP2_SAPOF, 292 amino acids (32.77 kDa); the protein from wheat is called **tritin**, database code S33631, 275 amino acids (29.58 kDa); that from *Phytolacca dodecandra* is **dodecandrin**, fragmentary data in database code S32971. Type II ribosome-inactivating proteins are enzymes with a similar action to the type I proteins, but have an additional covalently bound chain with lectin properties. They include **abrin**, **modeccin**, **ricin**, viscumin, and **volkensin**.

ribosome recycling factor *abbr.*: RRF; *formerly known as* **ribosome releasing factor**; a factor which, in bacteria is required for the recycling of ribosomes through decomposition of the termination complex following release-factor-mediated release of the completed polypeptide chain from the peptidyl tRNA. Example from *Escherichia coli*: database code RRF_ECOLI, 185 amino acids (20.61 kDa).

ribosyl *or* **ribofuranosyl** any **glycosyl** group formally derivable from the α- or the β-furanose forms of D- or L-ribose. (The pyranose forms of ribose are exhibited only by the uncombined sugar.)

ribosylate to add a ribosyl residue. *Compare* **ADP-ribosylation**.

ribosylthymine *an alternative name for* **ribothymidine**.

ribosylthymine monophosphate *an alternative name for* **ribothymidine monophosphate**.

ribosylthymine phosphate *an alternative name for* **ribothymidine phosphate**.

ribothymidine *or* **ribosylthymine** *symbol*: T *or* Thd; 5-methyluridine; thymine riboside; 1-β-D-ribofuranosyl-5-methyluracil; a rare ribonucleoside, found as a minor component of many species of transfer RNA, where it is present as a residue of its 5′-phosphate. *See also* **ribothymidine 5′-phosphate**. *Compare* **thymidine**.

ribothymidine monophosphate *or* **ribosylthymine monophosphate** *abbr.*: TMP; *the common name for* any ribothymidine phosphate, particularly for ribothymidine 5′-phosphate.

ribothymidine phosphate *or* **ribosylthymine phosphate** ribothymidine monophosphate *or* ribosylthymine monophosphate (*abbr.*: TMP); any phosphoric monoester or diester of ribothymidine. Of the three possible monoesters – the 2′-phosphate, the 3′-phosphate, and the 5′-phosphate – and the two possible diesters – the 2′,3′-phosphate and the 3′,5′-phosphate – only **ribothymidine 5′-phosphate** is of any significance (the locant therefore being omitted if no ambiguity may arise).

ribothymidine 5′-phosphate *or* **ribosylthymine 5′-phosphate** *or* **5′-ribothymidylic acid** *symbol*: Thd5′*P or* pT; *the alternative recommended names for* ribothymidine monophosphate or ribosylthymine monophosphate (*abbr.*: TMP); 5′-ribothymidylyl phosphate; thymine riboside 5′-(dihydrogen diphosphate); thymine (mono)ribonucleotide. (The locant is commonly omitted if there is no ambiguity as to the position of phosphorylation.) A residue of ribothymidylic acid occurs in many species of transfer RNA, where it is formed *in situ* by methylation of the uracil moiety of an existing uridylic acid residue. This modification is effected by tRNA (uracil-5-)-methyltransferase (EC 2.1.1.35), the methyl group being derived from *S*-adenosyl-L-methionine.

ribothymidylate **1** either the monoanion or the dianion of **ribothymidylic acid**. **2** any mixture of ribothymidylic acid and its anions. **3** any salt or ester of ribothymidylic acid.

ribothymidylic acid *the trivial name for* any phosphoric monoester of ribothymidine. The position of the phosphoric residue on the ribose moiety of a given ester may be specified by a prefixed locant – *see* **ribothymidine phosphate**. However, 5′-ribothymidylic acid is the ester commonly denoted, its locant usually being omitted if no ambiguity may arise. 5′-ribo-

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thymidylic acid is also an alternative recommended name for ribothymidine 5′-phosphate.

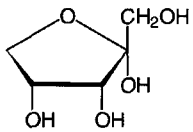
ribothymidylyl the ribothymidine[mono]phospho group; the acyl group derived from **ribothymidylic acid**.

ribovirus *an alternative name for* **viroid**.

ribozyme an RNA molecule with catalytic activity. Such activity was first discovered by Sidney **Altman** in 1981 for **RNase P**. Thomas R. **Cech** in 1982 discovered the catalysis by RNA of the reactions involved in the **splicing** of ribosomal RNA from *Tetrahymena*. In this reaction a 414-nucleotide **intron** is removed from a 6.4 kb precursor to yield the mature 26S rRNA molecule. A guanosine nucleotide is essential in the reaction, binding to the RNA and then attacking the 5′ splice site to form a phosphodiester bond with the 5′ end of the intron. After further reactions the 414-nucleotide intron is released and undergoes two further splicing reactions to produce a linear RNA of 395 nucleotides which has lost 19 nucleotides and is named L19. L19 is catalytically active and is a true enzyme acting both as a nuclease and a polymerase. The rate of conversion of a pentacytidylate into longer and shorter oligomers is about 10^{10} times the uncatalysed rate. Mg^{2+} plays an essential role. Much smaller ribozymes have been demonstrated, e.g. the **viroids** which infect plants and undergo self-splicing after replication. Comparisons of nucleotide sequences in the vicinity of specific cleavage sites suggest that the active site has a **hammerhead** secondary structure consisting of three helical regions radiating from a central core of unpaired nucleotides. mRNA precursors in the mitochondria of yeast and fungi also undergo self-splicing as do some RNA precursors in chloroplasts. Such reactions can be classified according to the nature of the unit that attacks the upstream splice site. Group I are mediated by a guanosine cofactor. In group II the attacking moiety is the 2′-OH of a specific adenylate of the intron. Such reactions resemble those that occur in the **spliceosomes**. The work on ribozymes has a special interest in respect of theories on the origin of life because those interested in the origin of life on earth favour the idea that the first macromolecules were composed of RNA. The fact that RNA can catalyse reactions lends support to their views. *See also* **ribonuclease**.

(Rib5)ppA *symbol for* adenosinediphosphoribose (alternative to Ado*PP*Rib *or* A5′pp5Rib).

D-ribulose *a nonsystematic name for* the ketopentose D-*erythro*-2-pentulose.



α-D-furanose form

D-ribulose 1,5-bisphosphate *abbr.*: RBP or RuBP; *former name*: ribulose diphosphate (*abbr.*: RDP or RuDP); a key metabolite of the **reductive pentose phosphate cycle**. It is formed in a reaction in which ribulose 5-phosphate is phosphorylated by ATP, catalysed by phosphoribulokinase, EC 2.7.1.19, and is a substrate of **ribulose-bisphosphate carboxylase**.

ribulose-bisphosphate carboxylase EC 4.1.1.39; *systematic name*: 3-phospho-D-glycerate carboxy-lyase (dimerizing); *other names*: ribulose-bisphosphate carboxylase/oxygenase (*abbr.*: Rubisco); the key enzyme in the fixation of CO_2 in the **reductive pentose phosphate cycle**; a copper protein. One molecule of D-ribulose 1,5-bisphosphate reacts with one molecule of CO_2 to yield two molecules of 3-phospho-D-glycerate, which can be converted into a hexose product (fructose 6-phosphate). If, as is possible, D-ribulose 1,5-biphosphate reacts with O_2 instead of CO_2, the products are one molecule each of 3-phospho-D-glycerate and 2-phosphoglycolate. This enzyme comprises up to 50% of leaf proteins and is the most abundant protein in the biosphere. Examples, all from tomato: large chain precursor: database code RBL_LYCES, 477 amino acids (52.62 kDa); small chain 1 precursor (less 17): database code RBS1_LYCES, 181 amino acids (20.28 kDa); small chain 2a precursor (less 5): database code RBS2_LYCES, 180 amino acids (20.25 kDa); small chain 3a/3c precursor: database code RBS3_LYCES, 180 amino acids (20.21 kDa); small chain 3b precursor: database code RBS4_LYCES, 180 amino acids (20.19 kDa).

D-ribulose 5-phosphate the 5-phosphate ester of D-ribulose; it is a component of the **pentose phosphate pathway**, the product of 6-phosphogluconate dehydrogenase. It is converted to ribulose 1,5-bisphosphate in the **reductive pentose phosphate cycle** of photosynthesis.

L-ribulose-phosphate 4-epimerase EC 5.1.3.4; an enzyme that catalyses the reaction:

L-ribulose 5-phosphate = D-xylulose 5-phosphate.

Example: *araD* gene product from *Escherichia coli*: database code ARAD_ECOLI, 231 amino acids (25.49 kDa).

Richner–Ranhart syndrome *see* **tyrosine transaminase**.

ricin a highly toxic lectin obtained from the seeds of the castor oil plant, *Ricinus communis*. It is a 493 amino-acid glycoprotein dimer comprising an A chain (M_r 66 000) and a B chain (M_r 34 000) linked by a disulfide bond. Ricin binds to the cell via interaction between the B chain and galactose groups on cell-surface receptors; then the disulfide bond is cleaved allowing the A chain to enter the cell. The A chain then binds to the proteins of the 60S ribosomal subunit, apparently in the region of binding of elongation factors eEF-1 and eEF-2, thereby halting protein translation. Protein from *R. communis* (precursor): database code RICI_RICCO, 576 amino acids (64.09 kDa). *See also* **abrin**, **ribosome-inactivating protein**.

rickets *or* **rachitis** a disturbance of calcium (and phosphate) metabolism in young growing animals (including humans), resulting from a deficiency of **vitamin D** or of its activation. It is characterized by softening of the bones and skeletal deformities, particularly bowing of the legs.— **rachitic** *adj.*

RID *abbr. for* radial immunodiffusion.

RIEP *abbr. for* rocket immunoelectrophoresis.

Rieske protein EC 1.10.99.1; *recommended name*: plastoquinol-plastocyanin reductase; *systematic name*: plastoquinol:oxidized-plastocyanin oxidoreductase; one of the four subunits of the cytochrome b_6–f complex. An enzyme that catalyses a reaction between plastoquinol-1 and two molecules of oxidized plastocyanin to form plastoquinone and two molecules of reduced plastocyanin. It is a high-potential 2Fe–2S protein. Example, precursor from tobacco: database code UCR1_TOBAC, 228 amino acids (24.12 kDa). Apart from the Rieske protein the subunits of the b_6f complex consist of **cytochromes b_6** and **f** and a 17 kDa peptide; it is similar to other iron–sulfur proteins (e.g. in mitochondria) and has three motifs.

rifampicin *or* **rifampin** an antibiotic, M_r 823, obtained as a semisynthetic derivative of rifamycin B, from which it differs only in the substituents on the ring marked X in the structure for that compound. It acts by inhibiting bacterial transcription, and is effective in sensitive bacteria (*see* **rifamycin**) at extremely low concentrations (0.01 μg ml^{-1}) while having no effect on eukaryotic transcription at 10^4 times that dose. Mitochondrial and chloroplast transcription may be affected at higher doses. It is stable when stored dry at 4 °C in the absence of light. In addition to its use as an antibiotic it has application in molecular biology as an agent for removing plasmids from bacteria in a process known as **plasmid curing**.

rifamycin any of a group of closely related anti-transcription antibiotics produced by *Streptomyces mediterranei* that are active against Gram-positive bacteria and *Mycobacterium tuberculosis* but are much less effective against Gram-negative organisms. Chemically and functionally they are closely re-

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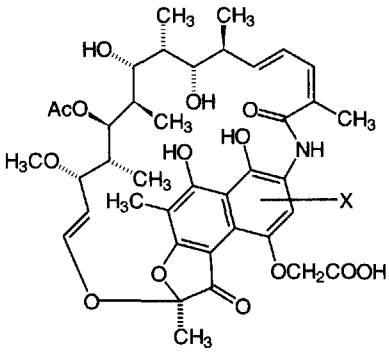
lated to the **streptovaricins**, and collectively the two groups are referred to as **ansamycins** – they are characterized by a chromophoric naphthohydroquinone nucleus spanned by a long aliphatic bridge. The mode of action of ansamycins involves inhibition of bacterial but not eukaryotic RNA synthesis via binding to the β subunit of bacterial DNA-dependent RNA polymerase and prevention of chain initiation; chain elongation is not affected once the initiation of RNA chain synthesis progresses beyond the third diester bond.



rifamycin B

rigid *(in lipid biochemistry)* a term sometimes used to describe the ordered phase of a lipid bilayer below the phase transition temperature. *See* **phase transition (of lipids)**.

Rimington, Claude (1903–93), British biochemist, distinguished for porphyrin research. With two coauthors he suggested (1968) that the British king, George III, suffered from variegate porphyria at a time preceding and during the American revolution. The hypothesis remains unproven and the cause of the king's deranged personality remains unknown.

rimorphin a 13-residue peptide that is a major Leu-enkephalin-containing peptide in tissues that contain **dynorphin** and α-neodynorphin. It yields three **enkephalin** sequences.

ring closure the formation of a covalent bond that converts a linear molecule into a ring structure.

Ringer, Sydney (1835–1910), British physician and physiologist who devised **Ringer's solution**.

Ringer–Locke solution *a less common name for* **Locke's solution**.

Ringer's solution *or* **Ringer solution** any of a number of aqueous solutions of mixed inorganic salts, of composition determined empirically by **Ringer** or adapted therefrom, that have been useful as fluid replacements *in vivo* or in place of serum as perfusing or suspending media for organs, tissues, or cells *in vitro*. Ringer's own mixtures (reported over the period 1882–87) were devised mostly for maintaining normal contractility of perfused isolated frog heart. One of the most effective solutions contained (in g L^{-1}, approx.) NaCl (7.0), KCl (0.04), $CaCl_2$ (anhydrous, 0.09), and $NaHCO_3$ (0.5). *See also* **Krebs' mammalian Ringer**, **Locke's solution**, **Tyrode's solution**.

Ringer–Tyrode solution *a less common name for* **Tyrode's solution**.

RING finger a **zinc finger** motif defined as

$$CX_2CX_{9-27}CXHX_2CX_2CX_{6-17}CX_2C$$

and present in a family of nuclear proteins.

ring opening the breaking of a bond that converts a ring structure to an open-chain form.

RIP *abbr. for* 1 repeat-induced point (mutation); a phenomenon found in *Neurospora*; when more than one copy of a DNA sequence is present in a haploid genome that goes through a cross, both ectopic and endogenous copies are subject to point mutation at a high rate. RIP occurs in the dikaryotic ascogenous hyphae. Because transformation of *Neurospora* typically leads to gene amplification, RIP provides a highly efficient and selective method of introducing mutations *in vivo* in any gene cloned *in vitro*. **2** ribosome-inactivating protein.

RISBASES proteins that have sequence similarity with members of the ribonuclease family but are thought not to function as ribonucleases. Examples are bovine seminal RNase and **angiogenin**. [From ribonuclease with special biological action.]

RIST *abbr. for* radioimmunosorbent test.

ristocetin a glycopeptide antibiotic complex from *Nocardia lurida*. Ristocetin A, M_r 2066, acts primarily on Gram-positive bacteria by inhibiting the biosynthesis of peptidoglycans, the mucopeptides of bacterial cell walls. Clinically, it is particularly useful against infections of the gut when administered by injection; however, it is ineffective when taken orally, and has toxic side effects including kidney damage.

Rittenberg tube an evacuable two-legged tube provided with a stopcock and used for the conversion of ^{15}N-labelled ammonium salts into dinitrogen prior to mass-spectrometric analysis. It has been jocularly known, especially in Israel, as **Rittenberg's trousers**. [After David Rittenberg (1906–70), US biochemist.]

R loop the structure formed when an RNA of complementary sequence stably base pairs with one of the DNA strands of double-stranded DNA, as happens at the start of **transcription**.

r.m.m. *abbr. for* relative molecular mass.

RMS *abbr. for* root mean square.

Rn *symbol for* radon.

RNA *abbr. and common name for* **ribonucleate** (def. 1) or **ribonucleic acid**; one of the two main types of **nucleic acid**, consisting of a long, unbranched macromolecule formed from ribonucleotides, the 3′-phosphate group of each constituent ribonucleotide (except the last) being joined in 3′,5′-phosphodiester linkage to the 5′-hydroxyl group on each ribose moiety of the next one. The presence of a free 2′-hydroxyl group on each ribose moiety renders these phosphodiester bonds susceptible to hydrolytic attack by alkali, in contrast to those of **DNA**. The RNA chain has polarity, with one **5′ end** and one **3′ end**. Two purines, adenine and guanine, and two pyrimidines, cytosine and uracil, are the major bases usually present. In addition, **minor bases** may occur; **transfer RNA**, however, contains unusual bases in relatively large amounts. The sequence of bases carries information, whereas the sugar and phosphate groups play a structural role. RNA is fundamental to **protein biosynthesis** in all living cells. **Messenger RNA** (mRNA) is responsible for carrying the coded genetic 'message', transcribed from DNA, to sites of protein assembly at the **ribosomes**. The latter are composed of **ribosomal RNA** (rRNA) plus proteins. A third species, transfer RNA (tRNA), is instrumental in importing amino acids to the assembly site, according to instructions carried by mRNA. In some viruses, RNA is the genetic material instead of DNA. Specific forms, functions, molecules, or preparations of RNA may be designated by prefixes or suffixes, thus: A-RNA *or* RNA-A, **A-form** of RNA; cRNA, **complementary RNA**; dsRNA, double-strand(ed) RNA; hnRNA *or* H-RNA *or* HnRNA, **heterogeneous nuclear RNA**; mRNA, **messenger RNA**; micRNA, **messenger-RNA-interfering complementary RNA**; mtRNA, **mitochondrial RNA**; nRNA, nuclear RNA; rRNA, **ribosomal RNA**; sRNA *or* S-RNA, **soluble RNA**; scRNA, small cytoplasmic RNA; snRNA, **small nuclear RNA**; snoRNA, **small nucleolar RNA**; ssRNA, single-strand(ed) RNA; tRNA, **transfer RNA**; tcRNA, **translational-control RNA**; *Z*-RNA *or* RNA-Z, **Z-form** of RNA.

RNA adenylating enzyme *see* **polynucleotide adenylyltransferase**.

RNAase *(sometimes) abbr. for* ribonuclease; RNase is more usual.

RNA-dependent DNA polymerase *another name for* RNA-directed DNA polymerase (*see* **reverse transcriptase**).

RNA-dependent RNA replicase *see* **RNA-directed RNA polymerase**.

RNA-directed RNA polymerase EC 2.7.7.48; *other name*: RNA nucleotidyltransferase (RNA-directed); an enzyme that

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catalyses a reaction between a nucleoside triphosphate and RNA_n to form RNA_{n+1} and pyrophosphates; it is required for the replication of RNA viruses; in the case of eukaryotic viruses, the enzyme normally comprises several subunits. Example from influenza virus (strain Ann Arbor), subunit P1 (or PB1): database code RRP1_IAANN, 757 amino acids (86.34 kDa); subunit P2 (or PA): database code RRP2_IAANN, 716 amino acids (82.71 kDa); subunit P3 (or PB2): database code RRP3_IAANN, 759 amino acids (85.99 kDa).

RNA–DNA virus *a former name for* **retrovirus**.

RNA helicase an ATP-dependent enzyme that is similar to **DNA helicase** except that its substrate is RNA. Example *dbpA* gene product (*Escherichia coli*) specific for 23S rRNA: database code DBPA_ECOLI, 457 amino acids (49.13 kDa).

RNA ligase (ATP) EC 6.5.1.3; *other name*: polyribonucleotide synthase (ATP); an enzyme that catalyses the reaction:

$$\text{ATP} + (\text{ribonucleotide})_n + (\text{ribonucleotide})_m = \text{ADP} + \text{pyrophosphate} + (\text{ribonucleotide})_{m+n}.$$

Example from bacteriophage T4: database code RLIG_BPT4, 374 amino acids (43.46 kDa). Example, tRNA ligase from yeast: database code TRNL_ YEAST, 827 amino acids (95.23 kDa).

RNA polymerase any enzyme that utilizes ATP, GTP, CTP, and UTP to synthesize RNA from a DNA or RNA template. DNA-dependent RNA polymerases include (i) the enzymes responsible for transcription of DNA and (ii) **primases**, which synthesize the RNA primers required for replication of DNA. An **RNA-directed RNA polymerase** (replicase or RNA synthetase) is involved in the replication of RNA viruses.

DNA-dependent (or DNA-directed) RNA polymerase (EC 2.7.7.6); *other name*: RNA nucleotidyltransferase (DNA-directed); it catalyses a reaction between a nucleoside triphosphate and RNA_n to form RNA_{n+1} and pyrophosphate. This EC class number includes the following examples.

In prokaryotes there is a single DNA-dependent RNA polymerase which transcribes all classes of DNA. The core *Escherichia coli* enzyme is composed of three types of subunit, α, β, and β′, and has the composition $\alpha_2\beta\beta'$; the holoenzyme contains an additional σ subunit or sigma factor. The core enzyme has a general affinity for DNA; sequence-specific DNA binding is conferred by the **sigma factor** which is responsible for promoter recognition and transcription initiation. Different sigma factors recognize different promoters. Following transcription initiation, the sigma factor dissociates from the core enzyme. The functions of the individual subunits are not fully understood. The β subunit is probably involved in binding ribonucleotide substrates; it is the target for **rifamycin** and **streptolydigin** antibiotics. The β′ subunit may bind template DNA. Examples: α subunit from *E. coli* (identical in *Salmonella typhimurium*): database code RPOA_ECOLI, 329 amino acids (36.47 kDa); β′ subunit from *E. coli*: database code RPOC_ECOLI, 1407 amino acids (154.98 kDa).

Phage RNA polymerases are much smaller and simpler than bacterial ones: the polymerases from phage T3 and T7 RNA, e.g., are single polypeptide chains of <100 kDa. Example from phage T3: database code RPOL_BPT3, 884 amino acids (98.68 kDa).

Eukaryotes have three types of DNA-dependent RNA polymerase in the nucleus, each producing a different type of RNA. RNA polymerase I, located in the nucleolus, synthesizes precursors of most ribosomal RNAs; RNA polymerase II, located in the nucleoplasm, synthesizes messenger RNA precursors; and RNA polymerase III, also located in the nucleoplasm, synthesizes the precursors of 5S rRNA, the transfer RNAs, and other small RNAs. These enzymes can be distinguished by their sensitivity to α-amanitin (*see* **amanitin**); class I enzymes are not inhibited by this octapeptide, whereas class II enzymes are rapidly inhibited by low concentrations; the sensitivity of class III enzymes varies depending on species. **RNA polymerase I** has 13 subunits totalling over 600 kDa; it recognizes a single type of promoter and requires at least two ancillary factors, UBF1 and SL1; it accounts for 50–70% of the RNA polymerase activity in eukaryotic cells. **RNA polymerase II** from all sources contains two large subunits of 215 and 139 kDa and several smaller polypeptides. The 215 kDa subunit has homology with the prokaryotic β′ subunit and contains a C-terminal domain (CTD) with multiple repeats of the consensus sequence YSPTSPS; the CTD is involved in initiation. The 139 kDa subunit has homology with the bacterial β subunit; the third largest subunit is related to the bacterial α subunit. Example of the latter: database code RPB3_YEAST, 318 amino acids (35.24 kDa). Three of the remaining subunits are common to RNA polymerases I, II, and III. Example: database code RPB5_YEAST, 215 amino acids (25.05 kDa). Most promoters used by RNA polymerase II contain the **TATA box**, which is recognized by the TATA-binding protein (TBP), a component of the **transcription factor** TFIID. Several other accessory factors are required for transcription by RNA polymerase II. **RNA polymerase III** has 14 subunits totalling 700 kDa. The promoters it uses may be upstream of the transcribed gene (for snRNAs) or within the gene (for tRNAs and 5S RNA). Three accessory factors, TFIIIA (a **zinc-finger** protein), TFIIIB, and TFIIIC, are involved in transcription from internal promoters. Examples: 47 kDa subunit of RNA polymerase III: database code RPC4_YEAST, 424 amino acids (46.89 kDa); 40 kDa subunit common to polymerases I and III; database code RPC5_YEAST, 335 amino acids (37.64 kDa).

Mitochondria and chloroplasts also contain RNA polymerase activity that synthesizes the RNAs required for mitochondrial and chloroplast protein synthesis. Polymerases from these organelles are smaller than the nuclear enzymes and more like prokaryotic RNA polymerases.

[RNA-polymerase]-subunit kinase EC 2.7.1.141; *other name*: CTD kinase (*abbr.* for C-terminal domain kinase); an enzyme that catalyses a reaction between ATP and [DNA-directed RNA polymerase] to form phospho-[DNA-directed RNA polymerase] and ADP.

RNase *usual abbr. for* ribonuclease; *compare* **RNAase**.

RNase MRP a site-specific endoribonuclease for mitochondrial RNA processing (hence 'MRP'). It contains an essential RNA component and cleaves mitochondrial RNA (mtRNA) transcripts that are complementary to the D-loop region of vertebrate mtDNA.

RNase P a catalytic activity responsible for the formation of the 5′-phosphate terminus of tRNA, by cleaving a sequence of bases from the 5′ end of a primary transcript, as a first step in the formation of pre-tRNA. The activity resides in the RNA moiety of a complex consisting of 86% RNA and 14% protein by weight. It was the first nonprotein enzymic activity to be discovered, by **Altman** – and is an example of a **ribozyme**. *See also* **ribonuclease**.

RNA synthetase an RNA-directed **RNA polymerase**.

RNA tumour virus a common designation for **retrovirus**, as this is the only group of RNA viruses known to cause cancer.

RNP *abbr. for* ribonucleoprotein. Specific kinds of RNP may be designated by prefixes, thus: hnRNP, **heterogeneous nuclear ribonucleoprotein**; scRNP, **small cytoplasmic ribonucleoprotein**; snRNP, **small nuclear ribonucleoprotein**.

Roberts, Richard J. (1943–), British molecular biologist; Nobel Laureate in Physiology or Medicine (1993) jointly with P. A. Sharp 'for their discovery of split genes'.

Robinson, (Sir) Robert (1886–1975), British organic chemist; Nobel Laureate in Chemistry (1947) 'for his investigations on plant products of biological importance, especially the alkaloids'.

Robison ester *an old name for* D-glucose 6-phosphate. *Compare* **Neuberg ester**. [After R. Robison, British chemist (1883–1941).]

Rochelle salt potassium sodium tartrate tetrahydrate; it is used as a constituent of **Fehling's solution**. [After La Rochelle, French port.]

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rocket immunoelectrophoresis *abbr.*: RIEP; a one-dimensional **electroimmunodiffusion**, *also known as* **electroimmunoassay**, used for quantitative analysis of proteins. Exact volumes of protein (antigen) solution are applied in an agarose gel of uniform thickness containing the corresponding antibody. An electric field causes the migration of both antigen and antibody. They react to form elongated curved precipitation lines, known as rockets because of shape, which are proportional in size to the amount of antigen. *See also* **crossed immunoelectrophoresis**.

Rodbell, Martin (1925–98), US biochemist; Nobel Laureate in Physiology or Medicine (1994) jointly with A. G. Gilman 'for their discovery of G-proteins and the role of these proteins in signal transduction in cells'.

rod cell *or* **rod** a rod-shaped cell that is one of the two types of light-sensitive cell of the vertebrate retina. Rod cells contain **rhodopsin** or (in freshwater and migratory fish and some amphibians) **porphyropsin**, and are responsible for vision in dim light. They occupy all of the margin of the retina and are absent from the fovea. Each rod photoreceptor is a highly specialized cell with an outer and inner segment, a cell body, and a synaptic region where the rod passes a chemical signal to retinal nerve cells. The phototransduction apparatus is in the outer segment, which contains a stack of disks, each formed by a closed stack of membrane in which rhodopsin molecules are embedded. The plasma membrane surrounding the outer segment contains cyclic-GMP-gated Na^+ channels. These are kept open in the dark by cyclic GMP molecules bound to the channels. Metarhodopsin II, an activated form of rhodopsin resulting from interaction with a photon, activates **transducin**, a **G-protein**, which then activates a cyclic GMP phosphodiesterase, reducing the cellular level of cyclic GMP to initiate a nerve impulse in the optic nerve. *Compare* **cone cell**.

rod gel a gel used in a form of polyacrylamide gel electrophoresis, in which the gel is cast in cylindrical glass tubes. Now largely superseded by slab-gel electrophoresis.

roentgen *a variant spelling of* **röntgen**.

rolling circle a mechanism for the replication of circular double-stranded DNA. One strand is nicked, then, using the unbroken strand as a template, the DNA is replicated around the circle. Replication does not cease when one circumference has been replicated, but continues around the circumference several more times (hence the name 'rolling'). Consequently, multimers of the replicon are produced in a long single strand with the appearance of a tail; this may then be cut into unit replicons, or into multimers containing tandemly repeated copies of the original unit; these may remain as single strands or be transcribed to yield a complementary strand.

röntgen *or* **roentgen** *symbol* R; the unit of **exposure** (def. 3) to X- or gamma radiation, expressed in terms of the amount of ionization caused in air. Defined originally (1928, 1937) as that quantity of radiation having a corpuscular emission per 0.001293 gram of air (equivalent of 1 cm^3 of dry air at stp) producing, in air, ions carrying one electrostatic unit quantity of electricity of either sign. Expressed in SI units, 1 R causes the production in air of ions (of one sign) carrying a charge of 2.58×10^4 C kg^{-1}; this corresponds to the formation of 1.61×10^{15} ion-pairs per kg of air and to an absorption of energy by air equal to 0.00869 J kg^{-1}. The energy absorption by water or tissue from 1 R of X- or gamma-radiation is about 0.0096 J kg^{-1}. Prior to 1956, the röntgen was used in clinical work to express both exposure and **absorbed dose**. *See also* **rad** (def. 2), **rem**, **rep**. [After Wilhelm Konrad von Röntgen (1845–1923), German physicist, discoverer of X-rays.]

röntgen equivalent man *or* **röntgen equivalent man** *see* **rem**.

röntgen equivalent physical *see* **rep**.

röntgen rays *a former name for* **X-rays**.

room temperature ambient temperature, often used for reactions that can be carried out on the bench without devices to maintain constant temperature. Normally within several degrees of 20 °C.

root effect the lowering of ligand affinity and of cooperativity of ligand binding (in hemoglobin) brought about by a low pH. [After R. W. Root who reported it in 1931.]

root mean square *abbr.* RMS; the positive square root of the mean of the squares of a series of values of x_i:

$$\text{RMS value} = \sqrt{\left(\frac{x_1^2 + x_2^2 + \ldots x_n^2}{n}\right)}$$

Compare **standard deviation**.

ROS *abbr. for* rod outer segment; *see* **rod cell**.

ROS a gene family encoding receptor-like tyrosine kinases of unknown function; v-*ros* is the oncogene of the acutely transforming avian sarcoma virus UR2 (named after the University of Rochester). The vertebrate gene product, Ros, has close similarity to the *Drosophila* **Sevenless protein**; it appears to be associated with a phosphoinositide response (*see* **phosphatidylinositol cycle**); Ros-1 is a member of the Src family. Example from chick: database code KROS_CHICK.

rosetting a method of isolating cells by allowing them to associate with red blood cells. For example, lymphocytes become surrounded with red cells, forming a 'rosette', and may then be isolated by sedimentation through **Ficoll** gradients.

rota-evaporate to evaporate a solution in a rotating round-bottomed flask in a temperature-controlled water bath, using an apparatus that can at the same time apply a vacuum to the flask interior. —**rota-evaporation** *n*.

rotamer *see* **rotational isomer**.

rotary evaporator an apparatus used for **flash evaporation**; *see also* **rota-evaporate**.

rotational correlation time *see* **correlation time**.

rotational diffusion rotation of a solute molecule around its centre of mass as a result of **Brownian movement**.

rotational frictional coefficient *see* **frictional coefficient**.

rotational isomer molecules of identical **configuration** may be distinguished as having different **conformations** after rotation about a bond. If an assembly of atoms X–A–B–Y (X and Y not being collinear with A–B) is viewed along the axis A–B, the X–A and B–Y bonds will make an angle with each other which may be 0° (superposition), 180° or some intermediate angle. This angle is termed the torsion angle, designated θ or ψ. Conformations are then described as synperiplanar (*sp*), synclinal (*sc*), anticlinal (*ac*) or antiperiplanar (*ap*) according as the torsion angle is within ± 30° of 0°, ± 60°, ± 120°, or ± 180°, respectively. Formerly, the terms *cis*, *gauche* and *trans* were in use for synperiplanar, synclinal and antiperiplanar respectively.

rotational strength *or* **rotatory strength** *symbol*: *R*; an index of the degree to which an **absorption band** exhibited by an optically active solute displays **circular dichroism**. It may be evaluated for the absorption band in question by means of the expression:

$$R = 2.296 \times 10^{-44} \int \left(\frac{\Delta\varepsilon_\lambda}{\lambda}\right) d\lambda$$

where λ is a wavelength of observation and $\Delta\varepsilon_\lambda$ is the difference between the molar (decadic) absorption coefficients of the left and right circularly polarized light beams at that wavelength. Rotational strength is thus essentially the absorption coefficient difference integrated over the entire absorption band.

rotation axis a crystal or an oligomeric protein molecule is said to possess an *n*-fold rotation axis if it presents exactly the same appearance after a rotation about that axis of 360°/*n*. *Compare* **screw axis**.

rotation–reflection axis *see* **symmetry**.

rotenone an insecticidal material and the active principle in derris. It is present in plants of the genera *Derris*, *Lonchocarpus*, *Tephrosia*, and *Mundulea*; these plants were used by indigenous peoples as fish poisons (*Derris* in Asia, *Lonchocarpus* in South America, and *Tephrosia* more extensively). Rotenone inhibits mitochondrial respiration on the oxygen side of the nonheme iron of NADH dehydrogenase. Extracts of rotenone-

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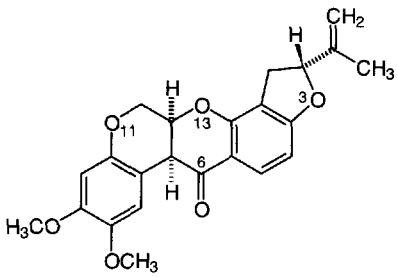
containing plants are used as insecticidal sprays and dusts (derris dust). *Compare* **piericidin A**.



Rot value *or* R_0t **value** a measure of the kinetic complexity of RNA based on its hybridization ability. The notation is a modification of R_0t, where R_0 is the initial RNA concentration and t is time. It is analogous to the Cot value (*see* C_0t) for DNA. $R_0t_{½}$ is the value corresponding to half complete association between complementary polynucleotides.

rough endoplasmic reticulum *abbr.*: RER; a region of the **endoplasmic reticulum** associated with ribosomes and involved in the synthesis of secreted and membrane-bound proteins. The nascent protein destined for secretion with its **signal peptide** associates with a receptor for the **signal recognition particle** and then translocates through the RER lipid bilayer by means of a group of proteins known as a **translocon**, which includes **TRAM**. The signal peptide is removed by the **signal peptidase**. The process is aided by **heat-shock proteins**, which serve as **chaperones**.

Round-up *see* **glyphosate**.

rousvirus *see* **retrovirus**.

rP the negative decadic logarithm of the molar concentration of inorganic phosphate; i.e. $rP = -\log[P_i]$. If, for the equilibrium

$$X + P_i = XP,$$

$$K = [X][P_i]/[XP]$$

then

$$rP = -\log K - \log([XP]/[X]).$$

RP-HPLC *abbr. for* reversed phase high-pressure liquid chromatography; *see* **reversed phase**.

R plasmid *abbr. for* resistance plasmid.

r-protein *abbr. for* ribosomal protein.

RP-TLC *abbr. for* reversed phase thin-layer chromatography; *see* **reversed phase**.

RQ *abbr. for* respiratory quotient.

RRM *abbr. for* RNA recognition motif; a conserved 80-amino-acid sequence motif present in members of a family of proteins that bind RNA. It has a β-α-β-β-α-β structure.

rRNA *abbr. for* ribosomal RNA; *see* **ribosome**.

(*RS*)- *prefix (in chemical nomenclature)* denoting a racemate containing a single chiral centre. *See* **sequence rule**.

R segment *abbr. for* repeat segment; part of retroviral RNA consisting of direct repeats i.e. repeats having the same orientation; the size of the repeated segments varies in different strains of virus, from 80 to 100 nucleotides.

***R/S* convention** the system of configuration specification of chiral compounds based on the **sequence rule**.

RSKG-5 *see* **tonin**.

R state *see* **R form**.

rtDNA *(sometimes) abbr. for* **recombinant DNA**; use not recommended.

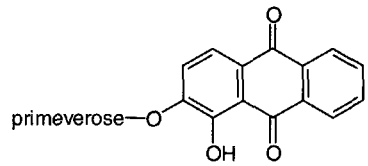
RTP *symbol for* any unspecified purine nucleoside 5′-triphosphate.

Ru *symbol for* ruthenium.

RU-486 *or* **RU-38486** mifepristone; 11β-(4-dimethylaminophenyl)-17β-hydroxy-17α-prop-1-ynylestra-4, 9-dien-3-one; a steroidal progesterone-receptor antagonist that prevents implantation of a fertilized ovum in the uterus. It is an effective contraceptive even when taken after coitus.

rubber a *cis*-1,4-polyisoprene with M_r varying from about 1×10^5 to 1×10^6, representing polymers of about 1500 to 60 000 **isoprene** residues. It is found in the latex of about 300 different flowering plants, but only *Hevea brasiliensis* is a commercial source. A nonelastic rubber from *Manilkara bidentata* latex is known as **balata**. It is a *trans*-1,4-polyisoprene.

ruberythric acid the glycoside; 2-alizarin β-D-primeveroside, a major component of the plant dyestuff madder.



rubidium *symbol*: Rb; a silvery-white metallic element of group 1 of the IUPAC **periodic table**; atomic number 37; relative atomic mass 85.48. Highly reactive, it must be stored in an inert atmosphere. Rb^+ may be used experimentally as a K^+ analogue (sometimes as substitute, othertimes as competitor).

Rubisco *abbr. for* ribulose-bisphosphate carboxylase.

RuBP *abbr. for* ribulose 1,5-bisphosphate.

rubredoxin *abbr.*: Rd; any of a group of bacterial **iron–sulfur proteins** that are small, highly conserved, contain non-heme iron, and are nonenzymic. They lack acid-labile sulfur, and are characterized by having either one or two iron atoms each entirely in mercaptide coordination, i.e. surrounded by four cysteine residues or sulfur-containing ligands. They are electron acceptors for, e.g., hydrogenase-linked redox processes and hydroxylase systems. Rubredoxins of M_r 6000–19 000 have been found in a number of bacteria. The ferric form is intense red, the ferrous form is colourless. Example from *Alcaligenes eutrophus*: database code RUBR_ALCEU, 78 amino acids (8.64 kDa). *Compare* **ferredoxin**.

rudimentary a gene that in *Drosophila* is the equivalent of ***pyr-1*** in a number of other eukaryotes. It encodes a **CAD protein**.

ruffled edge *or* **ruffling** the appearance of the leading edge of a moving cell in culture, caused by the extension of microspikes and lamellipodia, which when not attached to the substratum have the appearance of ruffles in flimsy dress fabric.

Russell's viper venom the venom of Russell's viper, *Vipera russellii*, a snake of SE Asia. It is used experimentally as a source of several enzymes especially phospholipases, proteases, and ribonucleases.

rusticyanin a blue copper-containing single-chain polypeptide obtained from a thiobacillus. It undergoes reduction during oxidation of Fe^{2+} with dioxygen. It is stable in acid, labile in alkali, and contains no arginine. Example from *Thiobacillus ferrooxidans*: database code RUS1_THIFE, 154 amino acids (16.38 kDa).

rutamycin *or* **oligomycin D** 26-demethyloligomycin A; an antifungal agent that has no significant activity against bacteria but is strongly inhibitory to a limited number of yeast and other fungal species. It acts by inhibiting mitochondrial ATPase F_1, preventing phosphoryl group transfer, but has no effect on isolated F_1 units. (Illustrated on p. 581.) *See also* **oligomycin**.

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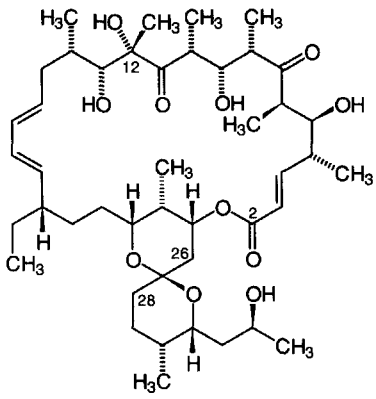
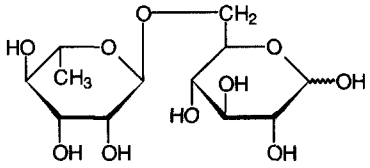


rutamycin

ruthenium red ruthenium oxychloride ammoniated; $[(NH_3)_5–Ru–O–(NH_3)_4–O–Ru–(NH_3)_5]Cl_6·4H_2O$. A brownish-red, water-soluble inorganic compound, used in microscopy and electron microscopy as a stain for acid mucopolysaccharides. It inhibits the influx of Ca^{2+} ions into mitochondria at extremely low concentrations.

rutinose the disaccharide, 6-*O*-*β*-L-rhamnosyl-D-glucose; it occurs in some glycosides, e.g. rutin, the 3′-rutinoside of **quercetin**.

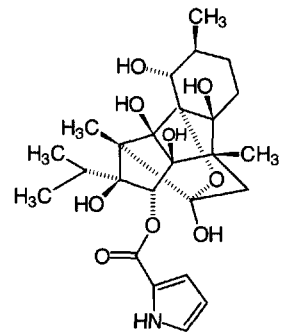


Ružička, Leopold (1887–1976), Croatian-born Swiss chemist; Nobel Laureate in Chemistry (1939) 'for his work on polymethylenes and higher terpenes' [prize shared with A. F. J. Butenandt].

***R*$_B$ value** *or* **relative band rate** *or* **relative band speed** *(in chromatography) symbol*: R_B; the ratio of the distance travelled by a zone of the substance of interest to the distance simultaneously travelled by a reference substance B. *See also* ***R*$_f$ value**.

***R*$_f$ value** *or* ***R*$_F$ value** *or* **band rate** *or* **band speed** *symbol*: R_f *or* R_F; *(in chromatography)* the ratio of the distance travelled by the centre of a zone of the substance of interest to the distance simultaneously travelled by the mobile phase. In paper and thin-layer chromatography, it is generally determined from the distance travelled by the substance from the origin and the distance travelled by the eluent front from the same point. [From 'rate relative to front'.]

ryanodine an alkaloid with insecticidal activity, isolated from *Ryania speciosa*. *See also* **ryanodine receptor**.



ryanodine receptor *abbr.*: RYR; any of a group of receptor proteins that bind **ryanodine**. They were first discovered in muscle, but subsequently identified in other cell types. Their natural role is to function as intracellular Ca^{2+}-release channels. In muscle, they provide communication between transverse tubules (**T-tubules**) and sarcoplasmic reticulum (SR); contraction of skeletal muscle is triggered by release of Ca^{2+} from SR following depolarization of T-tubules. The Ca^{2+} channel is modulated by Ca^{2+}, Mg^{2+}, and calmodulin. Three types are known: RYR1, the skeletal muscle type; RYR2, the cardiac muscle type; and RYR3, a highly truncated protein found in some nonmuscle cells. Cyclic ADP-ribose activates the RYR2 but not the RYR1 receptor. In muscle the receptors are integral transmembrane glycoproteins, probably tetrameric; the C-terminal region is on the SR lumen side of the membrane, while the N-terminal region (the major part of the molecule for RYR1 and 2) protrudes into the cytosol. Deficiency is associated with malignant hyperthermia. Example, skeletal muscle type from human: database code RYNR_HUMAN, 5032 amino acids (563.79 kDa).

RYN method a method for determining the plausibility of an **open reading frame**. A computational analysis of the sequence determines the frequency of the favoured codons R (purine), Y (pyrimidine), and N (anything). If these are found to be in the proportions expected from that normally found, it lends support to the fact that the correct **reading frame** has been selected, and that the open reading frame is correct.

RYR *abbr. for* ryanodine receptor.

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Ss

s *symbol for* **1** second (def. 1). **2** solid state (in a chemical equation). **3** atomic orbital corresponding to an orbital angular momentum quantum number (l) = 0. **4** singlet (in nuclear magnetic resonance spectroscopy). **5** strong absorption (in infrared spectroscopy).

s *symbol for* **1** sedimentation coefficient. **2** solubility. **3** *(in monosaccharide nomenclature)* the **septanose** form; it is suffixed to the symbol for the corresponding monosaccharide; e.g. glucoseptanose is symbolized as Glc*s*. **4** specific entropy (i.e. **entropy**/mass). **5** spin quantum number.

s- *abbr.: for* ***sec-***.

S *symbol for* **1** sulfur. **2** siemens. **3** Svedberg unit ($S_{w,20}$ is the symbol under standard conditions). **4** a residue of the α-amino acid L-serine (alternative to Ser). **5** a residue of an incompletely specified base in a nucleic-acid sequence that may be either cytosine or guanine. **6** a residue of the ribonucleoside **thiouridine** when the position of the thiol group in its thiouracil moiety is unknown or unspecified (alternative to sU *or* Srd). **7** substitution (reaction mechanism).

^{2}S *symbol for* a residue of the ribonucleoside 2-thiouridine (alternative to s^2U); *see* **thiouridine**.

^{4}S *symbol for* a residue of the ribonucleoside 4-thiouridine (alternative to s^4U); *see* **thiouridine**.

S_N1 *abbr. for* unimolecular nucleophilic substitution.

S_N2 *abbr. for* bimolecular nucleophilic substitution.

$S_{W,20}$ *see* **S** (def. 3).

S *symbol for* **1** entropy. **2** spin quantum number (of a system). **3** strangeness quantum number. **4** area (alternative to *A*).

S *stereochemical descriptor* denoting *sinister*; i.e. the absolute configuration of a chiral compound in which the priority (obtained using the Cahn–Ingold–Prelog sequence rules) of the substituent groups on the chiral centre decreases in an anticlockwise (left-handed) direction. For use as a prefix in chemical nomenclature, the descriptor is placed in parentheses and connected with a hyphen; e.g. (*S*)-alanine. For chiral compounds in which the relative but not the absolute configuration is known, *sinister* configuration is denoted by the prefix (*S**)-. *See* **sequence rule**. *Compare* ***R***.

S- *prefix (in chemical nomenclature)* denoting substitution on a sulfur atom in a compound; a particular sulfur atom may be specified by a right superscript.

-S *conformational descriptor* designating the **skew conformation** of a six-membered ring form of a monosaccharide or monosaccharide derivative. Locants of ring atoms that lie on the side of the structure's reference plane from which the numbering appears clockwise are indicated by superscripts preceding the letter, and those that lie on the other side of the reference plane by subscripts following the letter; e.g. 1,2-*O*-ethylidene-α-D-glucopyranose-$^1S_3$. *See also* **conformation**.

s.a. *abbr. for* specific activity.

SAA *abbr. for* serum amyloid A; *see* **amyloid A protein**.

SABP *abbr. for* secretory actin-binding protein.

saccharase *the trivial name for* any of a group of widely distributed hydrolases that attack the fructose (**fructosaccharases**) or glucose (**glucosaccharases**) end of appropriate oligosaccharides, liberating fructose or glucose respectively. The term is also used as an alternative trivial name for **invertase** (which is both a fructosaccharase and a glucosaccharase).

saccharate *see* **glucarate**.

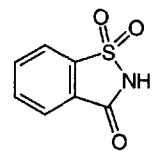
saccharic acid **1** *an old name for* **aldaric acid**. **2** *an old name for* glucaric acid; *see* **glucarate**.

saccharide any carbohydrate; the term is applied especially to the simple sugars, i.e. the **monosaccharides**, **disaccharides**, and short-chain **oligosaccharides**. *See also* **polysaccharide**.

saccharification the hydrolysis of sugar derivatives or complex carbohydrates to soluble, fermentable sugars.

saccharimeter an instrument for measuring the amount of sugar in a solution, especially a **polarimeter** used for such a purpose. *Compare* **saccharometer**.

saccharin 2,3-dihydro-3-oxobenzisosulfonazole; *O*-sulfobenzimide; an artificial, nonnutritive sweetening agent that is several hundred times sweeter than sucrose. It is often used as its more soluble sodium salt. Its carcinogenicity has been extensively studied. Rats receiving high doses produced tumours of the urinary tract but there is no clear-cut evidence of such an effect in humans.



saccharogenesis the process of producing soluble, fermentable sugars from a complex carbohydrate. —**saccharogenic** *adj.*

saccharogenic method a method for assaying amylase and similar enzymes that hydrolyse polysaccharides. It depends on determination of the amount of simple sugar product formed by the enzyme.

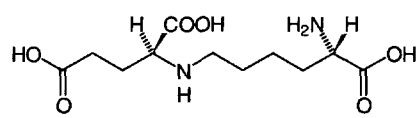
saccharometer an instrument for measuring the amount of sugar in a solution, especially a **hydrometer** specially calibrated for the purpose. *Compare* **saccharimeter**.

Saccharomyces a genus of budding yeasts that reproduce asexually by budding or sexually by conjugation. They are used especially as simple model organisms in the study of eukaryotic cell biology, and in genetic engineering. *Saccharomyces cerevisiae* is used commercially in bread-making and in the production of alcoholic beverages and industrial alcohol. It is able to divide vegetatively in either the haploid or diploid phase. This permits the isolation of recessive mutations in the haploids and complementation testing in the diploids. Transformation procedures that permit DNA uptake by either **protoplasts** or whole yeast cells have been developed and a wide range of cloning vectors constructed. In cases where a recombinant **glycoprotein** is desired, yeast has proved very useful since it can, unlike bacteria, effect post-translational **glycosylation**. It has been used for the production of a vaccine for hepatitis B.

saccharopine N^6-[1,3-dicarboxypropyl]-L-lysine; an intermediate in the **aminoadipic pathway** for lysine biosynthesis (e.g. in *Saccharomyces* spp., hence the name) and for lysine catabolism (e.g. in mammalian liver). The reactions involved are:

lysine + 2-oxoglutarate ⇌ saccharopine ⇌ glutamate + 2-aminoadipate 6-semialdehyde;

they are catalysed by **saccharopine dehydrogenases**, which are characterized as lysine-forming or glutamate-forming, and require either NAD$^+$/NADH or NADP$^+$/NADPH as coenzyme; *see* **saccharopine dehydrogenase (NAD$^+$, L-glutamate-forming)** and **saccharopine dehydrogenase (NAD$^+$, L-lysine forming)**.



saccharopine dehydrogenase (NAD$^+$, L-glutamate-forming) EC 1.5.1.9; an enzyme of the pathways for the synthesis and degradation of lysine. It catalyses the oxidation by NAD$^+$

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of N^6-(L-1,3-dicarboxypropyl)-L-lysine to L-glutamate and 2-aminoadipate 6-semialdehyde with formation of NADH. There is a second saccharopine dehydrogenase with the same reaction mechanism, in which the coenzyme is $NADP^+$: EC 1.5.1.10, saccharopine dehydrogenase ($NAPD^+$: L-glutamate-forming). *See also* **saccharopine**.

saccharopine dehydrogenase (NAD$^+$, L-lysine-forming) EC 1.5.1.7; *other name*: lysine–2-oxoglutarate reductase; an enzyme of the pathways for the synthesis and degradation of lysine. It catalyses the reaction between L-lysine, 2-oxoglutarate, and NADH to form N^6-(L-1,3-dicarboxypropyl)-L-lysine (**saccharopine**), NAD^+, and H_2O. Example from *Yarrowia lipolytica* (formerly *Candida lipolytica*): database code LYS1_YARLI, 369 amino acids (40.57 kDa). *See also* **saccharopine**.

saccharose *an old name for* **sucrose**.

safety cabinet a cabinet providing an area at bench level in which pathogenic agents may be handled or stored while preventing their entry into the atmosphere outside the cabinet; at the same time, sterility within the cabinet is normally ensured. Usually the cabinet is ventilated with a stream of air, which is extracted through a filter system that traps any pathogens. There are several grades of safety, the highest grades being for the more potentially hazardous materials; in the lowest grade, there is an inward flow of air through the front aperture; a higher grade cabinet is ventilated by a downward flow of filtered air, extracted so as to ensure also an inward flow through the front aperture, the extracted air being recirculated through the filter; in the highest grade, there is no front aperture, the operator manipulating the interior components using gloves mechanically sealed into the front of the cabinet.

SAH *abbr. for* *S*-adenosyl-L-homocysteine; *see* ***S*-adenosylhomocysteine**.

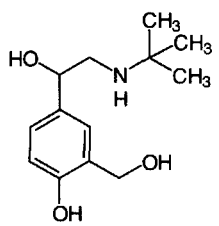
SAICAR *or* **SACAIR** *abbr. for* 1-(5-phosphoribosyl)-5-amino-4-(*N*-succinocarboxamide)-imidazole.

SAICAR synthetase *see* **phosphoribosylaminoimidazole-succinocarboxamide synthase**.

Sakaguchi test a test for guanidines; in alkaline solution they give a red colour with the **Sakaguchi reagent**, which contains α-naphthol and sodium hypochlorite. Arginine undergoes this reaction, as do arginine-containing proteins.

Sakmann, Bert (1942–), German physiologist; Nobel Laureate in Physiology or Medicine (1991) jointly with E. Neher 'for their discoveries concerning the function of single ion channels in cells'.

salbutamol *other name*: albuterol; 4-hydroxy-3-hydroxymethyl-α-[*tert*-butylamino)methyl]-benzyl alcohol, α^1-[[1,1-dimethylethyl)amino]methyl]-4-hydroxy-1,3-benzenedimethanol; a β-adrenergic agonist. The modification of the catechol ring by introduction of the hydroxymethyl group enhances the β_2-**adrenoceptor** activity by a factor of about 60 compared with **isoproterenol**.



salicylic acid 2-hydroxybenzoic acid; a white, crystalline, sweet-tasting substance, slightly soluble in water; its esters are found in bark of sweet birch and wintergreen, the leaves of which are used as a topical keratolytic and antifungal agent. It serves as a natural inducer of heat production ('**calorigen**') in *Arum* lilies, and has a broad regulatory role in plants. Its *O*-acetyl derivative is **aspirin**.

saline **1** of, concerned with, or containing common salt (sodium chloride). **2** of, or containing, salts of alkali metals or magnesium. **3** an aqueous solution of sodium chloride and (sometimes) other salts, of defined osmolarity, prepared for intravenous injection or perfusion; usually 0.9% w/v sodium chloride. *See also* **physiological saline**.

saliva the mixed secretions of the salivary glands and of the mucous membrane of the mouth. It contains an ***α*-amylase** (ptyalin), mucin, various inorganic ions, urea, buffers, lysozyme, etc., and has a pH near 7. It is secreted in response to food, which it serves to moisten and lubricate; the amylase may bring about some hydrolysis of ingested starch. *See also* ***sialic***. —**salivary** *adj.*

salivary gland any of the various glands that discharge **saliva** into the mouth. In humans there are three pairs: the parotid, sublingual, and submaxillary glands. In snakes they include the venom glands.

salivary juice the collective secretions of the salivary glands; i.e. **saliva**. Its secretion was studied by **Pavlov** and led him to the discovery of the conditioned reflex.

Salkowski test a test for the presence of cholesterol. When concentrated sulfuric acid is added to a chloroform solution of cholesterol, the chloroform layer shows a red to blue colour and the acid layer shows a green fluorescence. [After Ernst Leopold Salkowski (1844–1923), German physiological chemist.]

salmine a 6–7 kDa **protamine**, found in salmon sperm.

salmon *common name for* a number of fish of the family Salmonidae which live in coastal waters of the North Atlantic and North Pacific and breed in rivers. The flesh of these fish is comparatively rich in oils with a high content of long-chain *n*-3 **fatty acids**; typical composition (major fatty acids, expressed as % of total fatty acids): 16:0, 10; 16:1(*n*-7), 5; 18:0, 4; 18:1(*n*-9), 24; 18:2(*n*-6), 5; 18:3(*n*-3), 5; 20:1(*n*-9), 1; 20:4(*n*-6), 5; 20:5(*n*-3), 5; 22:6(*n*-3), 17.

Salmonella a genus of rod-shaped, motile, aerobic bacteria including the agents responsible for typhoid fever (*S. typhi*), some types of food poisoning, and other enteric diseases.

***Salmonella* mutagenesis test** *or* **Ames test** a method of screening chemicals for carcinogenicity, in which their mutagenic effect on selected strains of *Salmonella typhimurium* is evaluated – there being a high correlation between mutagenicity and carcinogenicity for substances of known action. The strains of *S. typhimurium* used are normally those that require histidine. They are plated out on histidine-deficient medium after being mixed with the potential mutagen. Mutations brought about by the test substance which reverse the defect in their ability to synthesize histidine are revealed by colonies growing on the plate.

salt **1** any member of a class of compounds formed, together with water, by reaction of an acid with a base (most commonly an inorganic acid and metallic base). **2** *or* **common salt** sodium chloride.

saltation **1** the action of jumping or leaping. **2** proceeding in a discontinuous manner by leaps interspersed by periods of rest. **3** an irreversible and inherited change in a cell or organism due to mutation. —**saltatory** *adj.*

saltatory conduction the passage of a nerve impulse across a gap, as between the nodes of Ranvier in a myelinated nerve fibre.

saltatory evolution evolution by sudden changes or by periods of active change with intervening inactive periods.

saltatory replication a hypothetical, sudden lateral replication of DNA thought to be responsible for the production of families of similar nucleotide sequences.

salt bridge **1** a tube, usually closed with porous plugs, that is filled with a solution of a salt (often potassium chloride, commonly saturated) and used to obtain electrical contact between two electrolytic half-cells without intermingling of their respective electrolytes. **2** any electrostatic bond between positively and negatively charged groups on amino-acid residues

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of a protein, that contributes to the stability of the protein structure.

salt fractionation the differential precipitation of proteins (or nucleic acids) from solution by the addition of neutral salts, often ammonium sulfate. *Compare* **salting out**.

salting in the increase in the solubility of certain proteins (e.g. globulins) and dipolar ions (e.g. cystine) produced in solutions of low ionic strength by an increase in the concentration of neutral salts.

salting out the decrease in the solubility of proteins, gases, uncharged molecules, and, in sufficiently concentrated solutions, electrolytes, produced in solutions of high ionic strength by an increase in the concentration of neutral salts.

salting-out chromatography a method of chromatography whereby water-soluble organic compounds are separated by ion-exchange chromatography by use of an aqueous salt solution as eluent.

salting-out constant *symbol*: K'_S; the slope of the straight line relating the logarithm of the solubility of a substance in neutral salt solutions and the ionic strength. It is given by

$$K'_S = -[\log(s/s^*)]/I,$$

where s is the solubility in mol dm^{-3} at ionic strength I, and s^* is the hypothetical solubility at zero ionic strength.

salt link *or* **salt linkage** an **ionic bond**.

salvage pathway any metabolic pathway that utilizes compounds formed in catabolism for biosynthetic purposes, despite these compounds not being intermediates in the corresponding normal biosynthetic pathways. Thus, free purine and pyrimidine bases may be converted to the corresponding ribonucleotides. In the case of purines, the ribose phosphate moiety of 5-phospho-α-D-ribosyl diphosphate (I) is transferred to the purine; thus

$$\text{adenine} + \text{I} = \text{adenylate} + \text{PP}_i.$$

See also **purine biosynthesis**.

SAM *abbr. for S*-adenosylmethionine.

SAMase *a trivial name for S*-adenosylmethionine cleaving enzyme (*S*-adenosylmethionine hydrolase; EC 3.3.1.2).

same-sense mutation *an alternative name for* **silent mutation**.

sample a small, separated portion of the whole. In experimentation it is often essential that the sample be fully representative of the characteristics of the whole (and always so for a **statistical sample**).

sample applicator a device to aid application of samples to chromatography plates, etc.

sample well a hole cut in an electrophoresis gel in which the sample to be analysed is placed.

sampling error *(in statistical analysis)* the chance difference between a measurement obtained from a **sample** and the corresponding measurement obtained from the whole population.

Samuelsson, Bengt Ingemar (1934–), Swedish biochemist; Nobel Laureate in Physiology or Medicine (1982) jointly with S. K. Bergström and J. R. Vane 'for their discoveries concerning prostaglandins and related biologically active substances'.

sandwich assay *or* **sandwich technique** a type of immunoassay in which antibody against the antigen to be assayed is bound to a solid surface (e.g. plastic). After addition of solution containing antigen the fixed antigen is washed. A second antibody, which is radioactive or fluorescent, is added, sandwiching the antigen; after removal of excess, the amount of bound label is determined. The second antibody may be specific for a different epitope on the antigen, thus enhancing overall specificity, or for the first antibody bound to an antigen.

sandwich complex a 2:1 macrocycle:cation complex in which the metal ion is held between two parallel macrocyclic **complexones**.

sandwich technique *an alternative name for* **sandwich assay**.

sandwich test an immunohistochemical procedure employing a **sandwich assay** to detect an antibody within a cell.

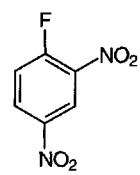
Sanfilippo syndrome A *an alternative name for* **mucopolysaccharidosis type IIIA**.

Sanfilippo syndrome B *an alternative name for* **mucopolysaccharidosis type IIIB**.

Sanger, Frederick (1918–), British biochemist, protein chemist, and nucleic-acid chemist; Nobel Laureate in Chemistry (1958) 'for his work on the structure of proteins, especially that of insulin'; Nobel Laureate in Chemistry (1980) jointly with W. Gilbert 'for their contributions concerning the determination of base sequences in nucleic acids' [prize shared with P. Berg].

Sanger's method **1** (for identifying and estimating N-terminal amino-acid residues of polypeptides and proteins) a method in which free unprotonated amino groups react with 1-fluoro-2,4-dinitrobenzene (FDNB). The dinitrophenylamino groups formed are stable to the acid used to hydrolyse the peptide bonds; the yellow arylated (DNP-) amino acids so released can then be identified by chromatography and estimated spectrophotometrically. **2** (for polypeptide and protein sequencing) a general method for deriving the primary sequence of a polypeptide chain, based on selective hydrolytic degradation of the chain into smaller peptides. The sequence of each smaller peptide may then be found by use of FDNB to label its N-terminal amino acid, together with total hydrolysis to give the amino-acid composition and further stepwise degradation by use of carboxypeptidase or by **Edman degradation**. By selection of different degradation procedures to ensure overlap of sequences between the various smaller peptides, the overall sequence of the starting material may be determined. **3** (for DNA sequencing) *an alternative name for* **chain-termination method**.

Sanger's reagent 2,4-dinitrofluorobenzene (*abbr.*: DNFB); 1-fluoro-2,4-dinitrobenzene (*abbr.*: FDNB); a substance used in structural protein chemistry to arylate free amino groups. *See* **Sanger's method** (def. 1, 2).



sapecin an insect **defensin** that is active against (mainly Gram-positive) bacteria. It has a high affinity for **cardiolipin**. Example (precursor includes presumed signal of unknown length) from *Sarcophaga peregrina*: database code SAPE_SARPE, 94 amino acids (9.90 kDa).

sapogenin any of the **aglycon** moieties of **saponins**; they may be steroids or triterpenes.

saponifiable fraction the portion of total lipid that, after treatment with hot alkali, is soluble in water and insoluble in ether.

saponifiable lipid any **lipid** that can be hydrolysed with alkali to give soap (fatty-acid salts) as one product; they include any **glycolipid**, **cholesteryl ester**, or **sphingolipid**.

saponification the hydrolysis of an **ester** by an alkali to give the alcohol and salt of the acid. Originally the term meant the hydrolysis of a neutral fat by alkali (e.g. potassium hydroxide) into glycerol and a soap. —**saponify** *vb.*

saponification equivalent the amount in grams of an ester that consumes one gram-equivalent of alkali in **saponification**. *Compare* **saponification number**.

saponification number the number of milligrams of potassium hydroxide consumed in the complete **saponification** of one gram of any particular fat, oil, or wax. *Compare* **saponification equivalent**.

saponin any member of a large group of glycosides, widely distributed in plants, that are powerful **surfactants**. Each saponin

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consists of an aglycon moiety (i.e. **sapogenin**), which may be a steroid or a triterpene, and a sugar moiety, which may be glucose, galactose, a pentose or methylpentose, or an oligosaccharide. All saponins foam strongly when shaken with water. They are membrane-active, powerful hemolytic agents and may be used at low concentrations to **permeabilize** cells. They are thus highly toxic on injection, but not on ingestion as they are not absorbed through the gut. *See also* **digitonin**.

saponin detoxifying enzyme an enzyme of unknown mechanism that acts, as the name implies, to prevent activity of antifungal **saponins**. Example from *Gaeumannomyces graminis avenacinase* (the so-called take-all fungus, an extreme pathogen of cereals): database code GGU17568, 637 amino acids (68.66 kDa).

sapor that which is sensed by taste; any quality relating to taste or savour. —**saporific** *or* **saporous** *adj.*

saporin a type I **ribosome-inactivating protein**, EC 3.2.2.22, from the soapwort *Saponaria officinalis*.

saposin *or* **sphingolipid activator protein** any of a group of peptide cofactors of enzymes for the lysosomal degradation of sphingolipids. They stimulate various enzymes, including glucosylceramidase, galactosylceramidase, cerebroside-sulfatase, α-galactosidase, β-galactosidase, and sphingomyelin phosphodiesterase. Saposins A to D are known. Deficiency of any may cause a mild form of a **sphingolipidosis** that normally results from deficiency of an enzyme the saposin activates. They contain characteristic domains known as saposin A-type or B-type domains. Example (precursor) from human: database code SAP_HUMAN, 524 amino acids (58.04 kDa). Specific polypeptides derived from this (amino acids in the precursor sequence in brackets) are as follows: saposin A (60–142) together with saposin C (311–391) stimulate hydrolysis of glucosylceramide by β-glucosylceramidase (EC 3.2.1.45) and galactosylceramide by β-galactosylceramidase (EC 3.2.1.46). Saposin C deficiency causes a variant of **Gaucher's disease**. Saposin B (195–274) is a homodimer and forms a solubilizing complex with the substrates of the sphingolipid hydrolases; deficiency causes a variant of **metachromatic leukodystrophy**. Saposin D (405–486) is a specific activator of sphingomyelin phosphodiesterase (EC 3.1.4.12) and deficiency causes a variant of **Tay–Sachs disease** (G_{M2} gangliosidosis). *See also* **swaposin**.

saprophyte any plant, fungus, or microorganism that lives on dead or decaying organic matter. —**saprophytic** *adj.*

sarafotoxin any of several toxic peptides that have been purified from the burrowing asp, *Atractaspis engaddensis*, and that cause cardiac arrest when injected into mice, probably as a direct result of coronary vasospasm arising from their strong vasoconstrictor activity. All have 21 amino acids, with two pairs of half-cystine residues in identical positions and a hydrophobic tail with a C-terminal tryptophan residue. They have strong homology with **endothelins** and have endothelin receptor agonist action. Sarafotoxins S6A–E are synthesized as a precursor from *A. engaddensis*: database code SRTX_ATREN, 543 amino acids (62.32 kDa). Sarafotoxin S6D has the sequence

CTCKDMTDKECLYFCHQDIIW.

See also **bibrotoxin**.

Saran Wrap *proprietary name for* a vinylidene chloride copolymer cling-film used for gel drying, food storage, and other purposes.

α-sarcin a cytotoxin produced by *Aspergillus giganteus*. It has ribonuclease activity, specific for purines in both single-stranded and double-stranded RNA. It inhibits protein synthesis, cleaving a single phosphodiester linkage between guanosine and adenosine residues in 28S rRNA in the 60S′ subunit of the eukaryotic ribosome, resulting in loss of 393 nucleotides from the 3′ end of 28S rRNA. This single site of action in the intact ribosome contrasts with its action on purified 28S rRNA, in which it causes extensive degradation, cutting on the 3′ side of every adenine or guanine. Example (precursor): database code RNAS_ASPGI, 177 amino acids (19.72 kDa), residues 1–27 being the signal, and 28–177 the enzyme.

sarcolemma the outer membrane of a muscle fibre. It consists of the plasma membrane, a covering basement membrane (about 100 nm thick and sometimes common to more than one fibre), and the associated loose network of collagen fibres. The term was originally used by light microscopists to designate the line visibly marking the outer fibre edge.

sarcoma a malignant tumour of connective tissue or of its derivatives. —**sarcomatous** *adj.*

sarcomere the functional unit of a myofibril of vertebrate muscle, about 2.3 μm long. In **striated muscle** the sarcomeres of many parallel myofibrils are positioned such that myosin **thick filaments** are aligned in register across the myofibril (having a dense appearance in microscopic preparations), as also are the actin **thin filaments** (which have a lighter appearance), resulting in the alternation of light, isotropic bands known as **I bands**, and dark, anisotropic bands known as **A bands**; the I band is bisected by a very dense, narrow **Z line**, while the central, less dense region of the A band is known as the **H zone**, which in turn is bisected by the dark **M line**, or midline, the location of specific proteins that link adjacent thick filaments to each other. The Z lines are due to attachment sites for thin filaments.

sarcoplasm all of the contents of a muscle fibre except nuclei. The sarcoplasm is pervaded by the **sarcoplasmic reticulum**. *Compare* **cytoplasm**. —**sarcoplasmic** *adj.*

sarcoplasmic reticulum *abbr.*: SR; a fine reticular network of membrane-limited elements that pervades the **sarcoplasm** of a muscle fibre. Like the endoplasmic reticulum the SR is continuous over large portions of the cell, it has a large surface-to-volume ratio, and is continuous with and/or homologous to the nuclear envelope. At the level of the I band (*see* **sarcomere**), the SR forms dilated sacs, or cisternae. Opposite the I bands and Z lines of every sarcomere there are always two SR terminal sacs that face each other across a narrow space, through which run **T tubules**. At the level of the A–I junction longitudinally orientated SR sacs run along the fibril, forming a palisade around the A band. The SR contains a Ca^{2+}-translocating ATPase that moves Ca^{2+} into the SR during ATP hydrolysis; ATP resynthesis is associated with movement of Ca^{2+} out of the SR vesicles.

sarcosine *N*-methylglycine; an intermediate in the conversion of choline, via betaine and dimethylglycine, to glycine, and in the synthesis of choline from glycine. *See also* **sarcosinemia**.

sarcosine dehydrogenase EC 1.5.99.1; a flavoprotein enzyme that catalyses the reaction:

$$\text{sarcosine} + \text{acceptor} + H_2O = \text{glycine} + \text{formaldehyde} + \text{reduced acceptor}.$$

The flavin is FMN.

sarcosinemia *or* (*esp. Brit.*) **sarcosinaemia** a rare inherited metabolic disease of humans, also found in ethylnitrosourea-induced mutants of mice, giving elevated plasma and urine levels of **sarcosine**. It may be accompanied by mental retardation or psychiatric disturbances. Primary sarcosinemia results from deficiency of **sarcosine dehydrogenase** (EC 1.5.99.1). Sarcosinemia may also be found in folate deficiency (*see* **folic acid**) in humans and in glutaric aciduria type II, but in primary sarcosinemia elevated levels of other organic acids are not found. Inheritance is probably autosomal recessive.

sarcosome a subcellular organelle found in muscle tissue that has essentially the same biochemical properties as a **mitochondrion** in other tissues. In muscles with intermittent activity, sarcosomes are found at the level of the I bands (*see* **sarcomere**); such muscles include skeletal muscles of vertebrates and invertebrates whose metabolism during activity is largely anaerobic. In muscles required to perform sustained activity, such as bird and insect flight muscles and vertebrate heart muscle, sarcosomes are found at the level of the A bands; these muscles have predominantly aerobic metabolism.

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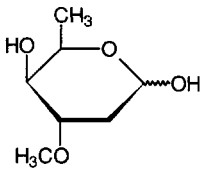
sarcotubule *another name for* **T tubule**.

sarin methylphosphonofluoridic acid 1-methylethyl ester; an **organophosphate** (def. 2) that inhibits acetylcholinesterase and other serine esterases. It is a military nerve gas but is useful in the treatment of leprosy and has some effect on AIDS.

D-sarmentose 2,6-dideoxy-3-*O*-methyl-D-*xylo*-hexose; a substance found as a component of some **cardiac glycosides**.



satellite DNA a fraction of DNA, present in most eukaryotic cells in amounts of up to 10% or more of total DNA, with a highly repetitive nucleotide sequence. Its base composition differs sufficiently from the bulk of the DNA to give rise to a 'satellite' band having a different buoyant density when DNA preparations, following **shear** force degradation, are centrifuged in cesium chloride density gradients. For instance, mouse satellite DNA contains about a million copies of a repeating sequence of approximately 300 base pairs with a lower (G+C) content than that of the moderately repetitive and unique DNA sequences. *See also* **minisatellite**.

satellite RNA small RNAs (≈350 bases) also called **virusoids**, found in plants; they are **encapsidated** by some plant viruses. *See also* **ribozyme**.

satellite virus a small virus that occurs in association with another virus, upon which it is dependent. An example is **satellite tobacco mosaic virus** (STMV). This 172 Å diameter particle encloses a 1059 nucleotide RNA that encodes only two proteins, the 159-residue viral coat protein and a 58-residue protein of unknown function. STMV can only multiply in cells that have been coinfected with tobacco mosaic virus. This is the only known example of such a parasitic relationship between a spherical virus and a rod-shaped virus.

saturable capable of undergoing **saturation** (def. 5). —**saturability** *n.*

saturated fatty acid any **fatty acid** in which the carbon–carbon bonds of the alkyl chain are exclusively single bonds. The predominant naturally occurring saturated fatty acids are **palmitate** and **stearate**; others include **laurate**, **myristate**, arachidate (*see* **arachidic acid**), behenate (*see* **behenoyl**), **lignocerate**, and cerotate (*see* **ceretoyl**). All saturated fatty acids can be derived metabolically from acetyl-CoA, both in animals and plants. *See also* **fatty-acid nomenclature**.

saturates *an informal term for* **saturated fatty acids**.

saturation **1** (of a chemical compound) the point at which all the valence bonds of the component atoms are satisfied, especially the state of an organic compound that contains only single carbon–carbon bonds. **2** (of a solution) the state in which it has the greatest concentration of the solute that can remain in stable equilibrium with undissolved solute at a given temperature and pressure. **3** (of a gas) the state in which there is the greatest concentration of the vapour associated with a liquid or solid that can remain in stable equilibrium with unvaporized liquid or solid, respectively, at a given temperature and pressure. **4** (of an active site of an enzyme or transporter) the point at which the site is fully occupied with ligand. Saturable enzyme or receptor systems exhibit hyperboliform or sigmoid curves of activity versus concentration (*see* **saturation kinetics**). **5** the act or process of bringing to or towards saturation; especially the addition of hydrogen to triple and double bonds.

saturation analysis *or* **binding assay** a development of **isotope dilution analysis** used for the measurement of very low concentrations of biologically potent substances (e.g. a specified hormone) in small samples of complex mixtures such as biological fluids. The essential steps of the technique are: (1) the substance, S, is allowed to react with a fixed amount of a specific binding agent under conditions such that the latter is always fully saturated with S; (2) the partitioning of S between the free and bound states is determined by the use of an indicator and by physical separation of the free from the bound form; and (3) the distribution of the indicator is compared with distributions obtained using a series of known amounts of S. The indicator is a labelled form of pure S, the label commonly being a radioisotope of high specific activity; alternatively, fluorescent, enzymic, or other labels may be used if they give the required sensitivity. The specific binding agent is generally an antibody (usually tailor-made), as in **enzyme immunoassay**, **fluoroimmunoassay**, or **radioimmunoassay**, or a naturally occurring macromolecular carrier or cellular receptor substance, as in **competitive protein-binding assay**.

saturation fraction *symbol*: y; the ratio of the concentration of bound ligand to the total concentration of the binding agent. Hence, in a binding reaction where a compound P binds X to form PX, then $y = [PX]/[P_{total}]$. A plot of y against [X] is known as the **adsorption isotherm** for this system.

saturation kinetics the kinetics of a reaction (or of **mediated transport**) when the velocity of the reaction (or of the transport) increases to a maximal value (plateau) as the concentration of the reactant (or of a component being transported) is increased.

saturation ratio *or* **cooperativity index** *symbol*: R_s; (of an allosteric protein) the ratio of the concentration of the substrate (or other small molecule) necessary to produce 90% of that required to produce 10% saturation of the specific sites on a protein. It is a convenient measure of the extent of cooperativity. *See also* **cooperative ligand binding**.

saxitoxin *abbr.*: STX; a paralytic poison, produced by the marine dinoflagellates *Gonyaulax catenalla* and *G. excavata*. It can be accumulated by shellfish, making them toxic when eaten. Its action is similar to that of **tetrodotoxin**, with which it competes for sodium channels.

Sb *symbol for* antimony.

SBH *abbr. for* sequencing by hybridization; a hypothetical method yet to be implemented for the very rapid sequencing of DNA. It is based on the idea of having all possible octamers (there are 63 536) on a small hybridization screen called a DNA chip. As the octamers form nested arrays, a DNA fragment (of a few hundred bases) would only hybridize to some of these and the sequence could be deduced computationally.

SBS model *or* **SBS** *abbr. for* side-by-side model.

sc *abbr. for* synclinal (def. 2).

s.c. *abbr. for* subcutaneous.

Sc **1** *symbol for* scandium. **2** *abbr. for* secretory component (*see* **secretory piece**).

SCAD *abbr. for* short-chain acyl-CoA dehydrogenase *or* butyryl-CoA dehydrogenase; *see* **beta-oxidation system**.

scaffolding protein any of a group of proteins that have specific binding sites and are instrumental in determining the structure and assembly of large three-dimensional structures such as a virus. Such proteins are integral to the **self-assembly doctrine** elaborated by Caspar and Klug.

scalar **1** a physical quantity, such as mass or time, that is characterized only by its magnitude and does not contain any concept of direction. **2** describable by a number representing a point on a scale undirected in space. *Compare* **tensor**, **vector** (def. 1).

scaler an electronic circuit or device that counts electrical pulses by aggregating the pulses and giving one output pulse for a predetermined number of input pulses.

SCAMP *abbr. for* secretory carrier membrane protein; it is a Ca^{2+}-binding protein with leucine zipper and zinc finger motifs. SCAMPs are widely distributed as components of post-Golgi membranes. They function in the mechanisms for recycling proteins between the Golgi and the cell surface. Ex-

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ample from rat, SCAMP 37: database code S37395, 338 amino acids (37.96 kDa).

scanner an instrument or device used to measure or sample the distribution of some quantity or condition in a particular system, area, or region, e.g. to measure the distribution of colour or radioactivity on a chromatogram or electrophoretogram, or to measure the radial distribution of light absorbance in a cell in an ultracentrifuge.

scanning electron microscope *abbr.*: SEM; *see* **electron microscope**.

scanning proton microprobe an instrument in which a sample is bombarded by a high-energy (1–4 MeV) proton beam, causing emission of X-rays that can be characteristically attributed to certain elements. The technique permits the detection of elements down to about 1 ppm.

Scatchard plot *a method of analysis of the binding of ligand* to a macromolecule (or receptor), based on the **Scatchard equation**, $\bar{\nu}/[L] = (n - \bar{\nu})K$, where $\bar{\nu}$ is the average number of ligand molecules bound per binding macromolecule, [L] is the free ligand concentration, n is the number of binding sites on the macromolecule and K is the intrinsic association constant. A plot is made of $\bar{\nu}/[L]$ on the y-axis and $\bar{\nu}$ on the x-axis. If the binding sites are identical and independent, a straight line is obtained of slope $-K$ with intercepts on the x-axis of n and on the y-axis of Kn. If there is interaction between the binding sites, or there are several classes of independent sites, the plot is not linear. [After George Scatchard (1892–1973), US physical chemist.]

scatter to disperse in random direction(s) by impact or other interaction, especially light, electrons, neutrons, or X-rays. The measurement of scattered rays or particles may lead to useful analysis, as in **light scattering**.

scatter diagram a graph upon which two measured characteristics of each individual of a population are represented by one dot.

scavenger *(in chemistry)* a substance that reacts with (or otherwise removes) a trace component, such as a trace metal ion, or that traps a reactive **reaction intermediate**.

SCF *abbr. for* stem cell factor.

Schally, Andrew Victor (1926–), Polish-born US biochemist and physiologist; Nobel Laureate in Physiology or Medicine (1977) jointly with R. Guillemin 'for their discoveries concerning the peptide hormone production of the brain' [prize shared with R. Yalow].

Schardinger dextrin *a former name for* **cyclodextrin**. [After Franz Schardinger (1853–1920), who first described such compounds in 1908.]

Schardinger enzyme *an alternative name for* **xanthine oxidase**.

Schardinger reaction the decolorization of Methylene Blue by milk in the presence of formaldehyde; the reaction is catalysed by **xanthine oxidase** (or Schardinger enzyme) in the milk.

Schatz, Albert (1920–), PhD student of S. A. **Waksman**, legally recognized as the co-discoverer of **streptomycin**.

Scheie syndrome *an alternative name for* **mucopolysaccharidosis I S**. [After Harold G. Scheie (1909–).]

Schiff, Hugo (1834–1915), German chemist who devised the reagent for aldehydes known as **Schiff reagent**.

Schiff base *or* **Schiff's base** any **imine** having the more limited general structure $R_2C{=}NR'$ where R may be any organyl group or H and R′ is any organyl group. It may be formed by condensation of the carbonyl group of an aldehyde or ketone with the amino group of a primary amine according to the equation:

$$R_2C{=}O + H_2NR' = R_2C{=}NR' + H_2O$$

Often considered to be synonymous with **azomethine**.

Schiff reagent a solution of leucofuchsin – fuchsin bleached with sulfurous acid – that produces a red colour when reacted with an aldehyde. The reagent is used in the **Feulgen reaction** and the **periodic acid–Schiff reaction**.

Schiff test **1** (for aldehydes) a test based on the red colour produced when aldehydes react with **Schiff reagent**. **2** (for uric acid) a test based on the reduction of silver ions (silver nitrate solution) to metallic silver by uric acid in sodium carbonate solution. **3** (for urea) a test based on the formation of a purple colour when urea is treated with a concentrated solution of furfural in concentrated hydrochloric acid solution. Allantoin, but not uric acid, also gives a positive test.

Schild equation the expected relationship between the **concentration ratio**, r, and the concentration of a reversible competitive antagonist, B. It is given by $r = [B]/K_B + 1$, where K_B is the dissociation equilibrium constant for the combination of B with the receptor. *Compare* **Gaddum equation**. [After Heinz Otto Schild (1906–84), Austrian-born British pharmacologist.]

Schild plot a plot of log (**concentration ratio** – 1) versus log concentration of antagonist. For a reversible competitive antagonist the plot has a gradient of 1. The intercept on the abscissa *then defines the concentration of antagonist required to* reduce the response of the target tissue (or organism) by half (the dissociation equilibrium constant: $-\log K_B = pA_2$ when the slope is exactly unity and there are no complicating factors; *see* **pA_2**).

Schilling test a test for cobalamin (vitamin B_{12}) malabsorption that depends on the oral administration of ^{57}Co- or ^{58}Co-labelled **cyanocobalamin** and measurement of the urinary excretion of the radioactive label during the ensuing 24 hours. [After Robert Frederick Schilling (1919–), US hematologist and nutritionist.]

schizophrenia any of a group of mental disorders characterized by a special type of personality disintegration, random thought processes, and impaired relation to reality. The biochemical basis of the disease remains enigmatic. Antipsychotic (neuroleptic) drugs such as **chlorpromazine**, which are widely used in the symptomatic treatment of all forms of schizophrenia, are considered to act by blocking postsynaptic dopamine D_2 receptors, though most are not totally selective in this action. —**schizophrenic** *adj.*, *n.*

Schizosaccharomyces pombe the fission yeast that is used to brew the African beer called *pombe*. The rod-shaped cells grow by elongation, and the spores germinate and divide as haploids. The arrangement of the membranous organelles, e.g. the Golgi apparatus, in fission yeast is closely similar to that of higher eukaryotes, in marked contrast to that of budding yeast. It is especially suitable for analysing the relationship between cell size and the cell cycle for two reasons: (1) the cells divide symmetrically, unlike budding yeast; and (2) the yeast grows in length but not in diameter.

Schlesinger test a qualitative test for **urobilin** in urine. The urobilinogen in the urine is first oxidized by iodine to urobilin, then a zinc–urobilin complex is formed by addition of zinc acetate in ethanol; the complex has a yellow-green fluorescence and an absorption band at 507 nm.

Schlieren method an optical method of exhibiting inhomogeneities in refractive index in transparent media, dependent on the deflection of a ray of light from its undisturbed path when it passes through a medium in which there is a solute inducing a gradient of refractive index normal to the ray. The curvature of the ray is proportional to the refractive-index gradient *in the direction normal to the ray. It is used in* biochemistry particularly in measurements of diffusion, sedimentation, and electrophoretic mobility of proteins and other substances. [From German *Schliere*, streak.]

Schmidt–Thannhauser procedure a method for the extraction and determination of DNA, RNA, and phosphoproteins. Material insoluble in dilute, cold trichloroacetic acid is dried, digested with alkali, and subsequently precipitated with a strong acid. The total phosphorus in the precipitate represents DNA, the soluble inorganic phosphorus represents the phosphoproteins, and the soluble organic phosphorus represents the RNA. [After Gerhard Schmidt (1901–81) and Siegfried Joseph Thannhauser (1885–1962), German-born US biochemist.]

Schoenheimer, Rudolf (1898–1941), German-born US biochemist; a leader in early work with isotopic tracers (^{2}H and ^{15}N) that led him (with colleagues) to put forward the concept

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of the **dynamic state of body constituents**, which became an important principle in metabolic regulation.

Schultz–Dale reaction an *in vitro* anaphylactic reaction in which the uterus or ileum of a sensitized animal (guinea pig) contracts specifically when a small amount of the sensitizing antigen is added to the bathing medium. The reaction is caused by histamine and similar substances that are released when the antigen combines with cellular antibody. [After H. H. **Dale**.]

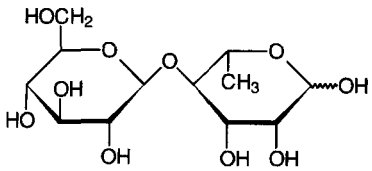
Schütz–Borrisow rule *or* **Schütz law** an empirical rule according to which the velocity of an enzyme reaction is proportional to the square root of the enzyme concentration. It was first developed for pepsin but applies only to the crude enzyme under certain limited conditions; similar results have been obtained with some other proteinases. The effect is due to the presence of a reversibly dissociating pepsin inhibitor in crude pepsin preparations.

Schwann cell a uninucleate cell of the **neurilemma** surrounding a myelinated neuronal axon that is responsible for the formation and maintenance of the **myelin sheath** in peripheral myelinated neurons. [After Theodor Schwann (1810–82), German anatomist and physiologist.]

Schwannomin *see* **merlin**.

SCIF *abbr. for* secondary cytotoxic T-cell-inducing factor (i.e. **interleukin 2**).

scillabiose the disaccharide 4-*O*-*β*-D-glucopyranosyl-L-rhamnose; it occurs in a **glycoside** of *Scilla maritima*.



scinderin *or* **adseverin** a Ca^{2+}-dependent cytosolic actin filament severing protein present in chromaffin cells, platelets, and a variety of secretory cells. Example (bovine): database code BBSCINDE, 715 amino acids (80.68 kDa).

scintillant **1** (of a phosphor) exhibiting scintillation. **2** *a jargon term for* **scintillator**.

scintillate **1** to give off sparks, to sparkle. **2** (of a phosphor) to emit quanta of light discontinuously, by fluorescence, when struck by a charged particle or a high-energy photon.

scintillation **1** the act of scintillating. **2** the flash of light produced in a phosphor when it is struck by a charged particle or a high-energy photon.

scintillation autoradiography *an alternative term for* **fluorography** (def. 2).

scintillation cocktail *or* **scintillation fluid** any mixture, containing a **scintillator**, to which **beta emitters** can be added for the purpose of **scintillation counting**; the radiation excites the scintillator to emit light. Many scintillation cocktails are based on hydrophobic solvents, since for the most part scintillators sparingly soluble in aqueous solutions have been used. The first scintillator to be widely used was 2,5-diphenyloxazole (PPO), often used in conjunction with 1,4-bis(5-phenyl-2-oxazolyl)benzene (PoPoP), which is excited by the light emitted by PPO to emit light of a higher wavelength more suitable for measurement. Subsequently many other scintillators, especially biodegradable compounds and others more compatible with water, have been developed. *See also* **biphenylylphenyloxadiazole**, **bismethylstyrylbenzene**.

scintillation counter an instrument for the detection and measurement of the intensity of high-energy radiation. Instruments for detecting gamma radiation contain a detector, normally a crystal of sodium iodide containing a small amount of thallium, and this is encased in a metal 'top hat' lined with a white reflector, the open end being sealed with Perspex. When the sodium iodide absorbs γ rays it emits a flash of light. For the counting of β^- emissions, the radioactive substance is dissolved or suspended in a **scintillation cocktail** contained in a glass or plastic vial, which is inserted into a chamber in the counter. Sometimes a solid scintillant is used for this also, e.g, for the effluent from chromatography columns. In the case of both types of instrument, the flashes of light produced are detected by a photomultiplier and converted into pulses of electric current which may be counted by an electronic counter.

scintillation fluid *an alternative term for* **scintillation cocktail**.

scintillation spectrometer *another name for* **scintillation counter**.

scintillator *or* **scintillant** any phosphor that fluoresces when struck by a charged particle or a high-energy photon. *See* **scintillation cocktail**.

scintillon a subcellular, crystal-like structure, found in bioluminescent organisms, that emits light on acidification in the presence of oxygen.

scissile capable of being split easily or cut smoothly, especially of an easily cleaved chemical bond.

scission a division or splitting; an act of dividing a nonisometric object orthogonally to its longest axis, especially a chemical bond or a fibrous molecule; **cleavage** (def. 2).

scleral pertaining to the sclera, the fibrous outer layer of the eyeball.

scleroprotein any of a group of simple, generally fibrous proteins that are insoluble in aqueous solutions; examples include **keratin** and silk **fibroin**.

sclerosis hardening of a tissue as a sequel to inflammation; especially an increase of connective tissue in the nervous system. *See also* **arteriosclerosis**. —**sclerotic** *adj.*

scopolamine *see* **hyoscine**.

scorbutic of, pertaining to, or affected with **scurvy**.

scotophobin a 15-residue peptide that accumulates in the brains of rats trained to avoid the dark; administration is said to elicit a similar response in untrained animals. It is thought to be the first memory-directing substance isolated and identified.

scotopia adaptation to darkness; the adjustment of the eye to vision in dim light or the dark. It is considered to involve mainly retinal **rod cells**. *Compare* **photopia**. —**scotopic** *adj.*

scotopsin an **opsin** that is the apoprotein of a **rhodopsin**.

SCP *abbr. for* single-cell protein.

scrapie a **spongiform encephalopathy** of sheep and goats, and the first to be identified of a group once thought to be 'slow virus' infections occurring naturally and caused by an unconventional agent. Scrapie has similarities to two other animal diseases, transmissible mink encephalopathy and **bovine spongiform encephalopathy**, and three transmissible human dementias, **kuru**, **Creutzfeldt–Jakob disease**, and **Gerstmann–Sträussler syndrome**. All these diseases are now accepted as being caused by alterations in the **prion proteins** in the nervous system. The disease has been known since its first reported occurrence in merino sheep in Spain in 1732, which was rapidly followed by reports of other cases in Britain and Germany. The incubation period for the scrapie agent is usually 1–3 years. Different breeds of sheep exhibit markedly different susceptibilities to scrapie. As many as 20 different strains of scrapie agent, each with distinct properties in terms of incubation period in a given host and location of damage within the brain have been identified and transferred to mice. It would appear that the strains are passed to the progeny, so any explanation of the nature of the infective agent and process must take this into account.

screen **1** to protect from; esp. from harmful agents or radioactivity using sheets of lead, glass, or plastic; or from radiofrequency interference using a copper sheath or wire net. **2** to sift data, often using a limited or general assay, for selection of a particular phenomenon or result; samples selected by preliminary screening can be isolated for more detailed study. **3** *(in clinical chemistry)* to carry out any diagnostic procedure on a

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large cohort of patients with a view to detecting hitherto asymptomatic disease; *see also* **genetic screening**. **4** any device or material that acts to screen.

screw axis a crystal or an oligomeric protein molecule is said to possess an *n*-fold screw axis if it presents exactly the same appearance after rotation about that axis of 360°/*n* coupled with a translation parallel to the axis. *Compare* **rotation axis**.

scRNA *abbr. for* small cytoplasmic RNA.

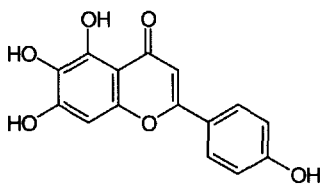
scRNP *abbr. for* small cytoplasmic ribonucleoprotein.

scurvy avitaminosis C; a deficiency disease caused by lack of **ascorbic acid** (vitamin C) in the diet. It is characterized by anemia, sponginess and ulceration of the gums, hemorrhages into the skin and subcutaneous tissues, and delayed wound healing.

scute a gene in *Drosophila* for **AS-C protein**.

scutelarin EC 3.4.21.60; *other name*: taipan activator (being from the venom of the taipan (snake), *Oxyuranus scutellatus*). An enzyme that catalyses the selective cleavage of Arg-|-Thr and Arg-|-Ile in prothrombin to form **thrombin** and two inactive fragments; its specificity is similar to that of factor Xa (*see* **blood coagulation**). *Compare* **scutellarin**.

scutellarein 4′,5,6,7-tetrahydroxyflavone; the aglycon of scutellarin. *Compare* **scutelarin**.



scutellarin the glucuronide of **scutellarein**, from *Scutellaria* spp. *Compare* **scutelarin**.

scyrp *colloquialism for* scRNP (i.e. **small cytoplasmic ribonucleoprotein**).

SD *abbr. for* standard deviation.

SDS *abbr. for* sodium dodecyl sulfate.

SD sequence *abbr. for* Shine–Dalgarno sequence.

SDS–PAGE *abbr. for* SDS–polyacrylamide gel electrophoresis.

SDS–polyacrylamide gel electrophoresis *or* **SDS gel electrophoresis** *abbr.*: SDS–PAGE; a rapid and inexpensive method for resolving a protein into its subunits and determining their relative molecular masses (M_r values), based on the ability of **sodium dodecyl sulfate** to cause dissociation of oligomeric proteins and to bind to the subunits to form complexes of constant charge-to-mass ratio. On **zone electrophoresis** in polyacrylamide gel, such complexes often have mobilities directly related to their M_r values, which, if unknown, may thus be obtained by comparison with standards. *Other name*: detergent gel electrophoresis.

Se *symbol for* selenium.

SE *abbr. for* standard error; *see* **standard error of estimate of the mean**.

SEA a gene family encoding membrane receptor tyrosine kinases having strong homology with the **insulin receptor** family. The acutely transforming virus, avian erythroblastosis virus (*abbr.*: AEV) strain 13, contains the oncogene v-*sea*; this transforms fibroblasts and erythroblasts, but not avian myeloid cells. Sea, the product of c-*sea*, the cellular homologue of v-*sea*, phosphorylates Shc (*see* ***SHC***) on tyrosine residues. Example from AEV strain 13: database code KSEA_AVIET, 370 amino acids (41.70 kDa).

sealase *a former name for* DNA ligase (ATP); *see* **DNA ligase**.

sea-urchin-hatching proteinase *see* **envelysin**.

sebaceous gland any of the single or branched glands in the skin that produce the oily substance, **sebum**. They open into the hair follicles.

sebum the oily secretion of the sebaceous glands in the skin. It contains lipids such as waxes, squalene, and triacylglycerols; the triacylglycerols are broken down by anaerobic bacteria during secretion to form fatty acids. Sebum helps to form an effective barrier against water loss.

sec *symbol for* **secant** (def. 1).

sec. *abbr.* and *obsolete symbol for* **second** (def. 1).

sec- *abbr.*: *s-*; *prefix (in chemical nomenclature)* signifying **secondary** (def. 1a).

secant **1** *abbr. and symbol*: sec; the reciprocal of the **cosine** of an angle. **2** a straight line cutting a curve at two or more points.

seco- *prefix (in chemical nomenclature)* denoting cleavage of a ring with addition of one or more hydrogen atoms at each terminal group thus created. The numbering of the skeletal atoms of the parent molecule is retained.

seco-carotenoid a **carotenoid** in which one of the rings has undergone fission by breakage of a carbon–carbon bond; e.g. semi-β-carotenone (5,6-seco-β-β-carotene-5,6-dione).

second **1** *symbol*: s; the SI base unit of time, equal to the duration of 9 192 631 770 periods of the radiation corresponding to the transition between the two hyperfine levels of the ground state of the caesium-133 atom. **2** *symbol*: ″; a unit of plane angle equal to 1/60 of a minute; i.e. 4.848 14 microradian (π/648 000 rad). *See* **angle** (def. 1).

secondary *(in chemistry)* **1** *prefix*: *sec-* (*abbr.*: *s-*); describing an alkyl compound (e.g. an alkanol) in which the functional group (e.g. a hydroxyl group) is attached to a carbon atom linked to two others. **b** describing the carbon atom bearing the functional group in such a compound. **2** describing an amide or amine in which two appropriate groups are attached to a nitrogen atom. **3** describing a salt formed by replacing two of the ionizable hydrogen atoms of a tribasic acid by one or two other cations of appropriate valency. *Compare* **primary**, **tertiary**.

secondary bond *a loose term to describe* any of the weak attractive forces between atoms and/or molecules, especially when these stabilize a three-dimensional structure. It includes **hydrogen bonds**, **hydrophobic interactions**, and **van der Waals forces**.

secondary cell wall deposition *(in plants)* the deposition of microfibrils and noncellulosic polysaccharides on the primary cell wall. It provides additional conducting and supporting tissue and frequently makes up the greater part of the mature cell wall.

secondary charge effect an effect seen in the hydrodynamic study of charged macromolecules when the positive and negative ions of the supporting electrolyte have different sedimentation (or diffusion) coefficients, leading to the establishment of local electric fields due to charge separation. These local fields act as an additional force on the macromolecules, either accelerating or retarding their movement.

secondary cytotoxic T cell-inducing factor *abbr.*: SCIF; *an alternative name for* **interleukin 2**.

secondary deficiency a nutritional deficiency occurring when the dietary content of some essential nutrient is known to be adequate in normal conditions. It may be caused by a failure of absorption from the gut due to disease, diminished synthesis of a vitamin by the intestinal flora during treatment with an antibacterial agent, or increased requirement, e.g. in pregnancy.

secondary electron an electron emitted from a solid as a result of the impact of another electron. If the energy of the incident primary electron is sufficient, more than one secondary electron may be emitted, an effect exploited in an **electron multiplier**. *See also* **photomultiplier**.

secondary emission the phenomenon of emission of **secondary electrons**.

secondary F′-containing strain *see* **F′ plasmid**.

secondary fluor a second fluorescent agent that absorbs the fluorescent light emitted by a **primary fluor** and is thus excited to emit light at a higher wavelength, which may be more convenient for detection.

secondary hyperlipidemia *see* **hyperlipidemia**.

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secondary immune response an immune response to an **immunogen** to which an animal has previously been exposed and to which its lymphoid tissue has been primed. It consists characteristically of the rapid production of large amounts of **antibody** over a few days, following which the level of antibody slowly declines in an exponential manner. *Compare* **primary immune response**.

secondary lysosome *or* **phagolysosome** a **lysosome** that contains not only the specific acid hydrolases but also their substrates taken up from the environment or sequestered from the cell's own cytoplasm. Secondary lysosomes are formed by fusion of a **primary lysosome** with a **phagosome** or a vesicle containing endocytosed matter. *Compare* **telolysosome**.

secondary messenger *a variant form of* **second messenger**.

secondary metabolism the formation of end products of metabolism – **secondary metabolites** – that often have no readily apparent use in the producing organism.

secondary metabolite any of a group of chemically very diverse natural products that have a restricted taxonomic distribution, usually possess no immediately obvious function in cell growth, and are often (but not always) synthesized by cells that have stopped dividing; typically they exist as members of closely related chemical families, usually of M_r < 1500, but some bacterial toxins are considerably larger. An example of a secondary metabolite is penicillin.

secondary response *see* **secondary immune response**.

secondary structure **1** (of a protein) the arrangements of the polypeptide chain that form more-or-less regular hydrogen-bonded structures, in particular α-helical and β-pleated sheet structures; *see* **alpha helix**, **beta strand**. **2** (of a nucleic acid) the arrangement of one or two polynucleotide chains in bihelical structures, stabilized by hydrogen bonds between complementary bases (*see* **complementary base sequence**); *compare* **clover-leaf structure**. *See also* **primary structure**, **quaternary structure**, **tertiary structure**.

second law of thermodynamics *see* **thermodynamics**.

second messenger *or* **secondary messenger** a mediator that is caused to accumulate in an effector (target) cell by the action of a **hormone**, **growth factor**, or other agonist, and that brings about the action of that agonist on the cell. The major second messenger systems are currently recognized to include: synthesis of cyclic AMP by **adenylate cyclase** (the first of such systems to be discovered); synthesis of cyclic GMP by **guanylate cyclase**; opening of **ion channels**; the phosphoinositide system, (*see* **phosphatidylinositol cycle**) involving activation of phosphoinositide-specific phospholipase C (*see* **phospholipase**), or **1-phosphatidylinositol 3-kinase**; and protein phosphorylation by serine/threonine-specific or tyrosine-specific **protein kinases**. An important component in several of these systems involves coupling of activated receptor to the effector system through a **G-protein**.

second-order rate constant *see* **rate constant**.

second-order reaction *see* **order of reaction**.

seco-steroid a **steroid** in which one of the rings has undergone fission by breakage of a carbon–carbon bond.

secretagogue *or* **secretogogue** an agent that stimulates secretion (usually of a named hormone, juice, or other glandular product). *See also* **+agogue**.

secretase a type of enzyme that cleaves the extracellular domain of a number of membrane proteins of type I or type II topology, releasing the extracellular part of the protein into the circulation. Cleavage normally occurs close to the extracellular face of the membrane. Proteins on which secretases act include Alzheimer's amyloid precursor protein, angiotensin converting enzyme, transforming growth factor-α, and the tumour necrosis factor ligand and receptor superfamilies. Secretase activity is inhibited by a number of metalloproteinase inhibitors, suggesting that secretases may be metalloproteinases.

secrete to elaborate and emit a **secretion** from a cell or, particularly, from a gland.

secretin a digestive hormone, discovered in 1902 by William Maddock Bayliss (1860–1924, British biologist) and Ernest Henry Starling (1866–1927, British physiologist) (the first hormone to be discovered). It has the sequence (human):

HSDGTFTSELSRLREGARLQRLLQGLV-NH_2

(3.04 kDa), and is formed from a 134-amino-acid precursor, which is synthesized in specific endocrine cells, S cells, in the mucosa of the small intestine. It stimulates the release of bicarbonate, enzymes, and potassium ions from the pancreas and stimulates the secretion of enzymes and electrolytes in the gut; it also inhibits HCl production by the stomach. Secretin lends its name to a superfamily that on structural grounds includes **gastric inhibitory peptide**, **GHRH**, **glucagon**, **peptide HI**, and **vasoactive intestinal polypeptide**. Example of precursor from *Mus musculus*: database code SECR_MOUSE, 133 amino acids (14.91 kDa).

secretin receptor any of several membrane proteins that bind **secretin** and mediate its intracellular effects. These are seven-transmembrane-domain, G-protein-coupled, adenylate cyclase stimulating receptors, not structurally related to other G-protein-coupled receptors. Example from human (precursor): database code SCRC_HUMAN, 440 amino acids (50.23 kDa).

secretion **1** the process of elaborating, segregating, and emitting a substance or juice from a cell, organ, or organism; e.g. the secretion of insulin by the B cells of the islets of Langerhans, or the secretion of urine by the kidneys. At the cellular level there are three basic types of secretion: **apocrine**, **holocrine**, and **merocrine**. **2** a product of **secretion** (def. 1) from a cell, organ, or organism.

secretogogue *a variant spelling of* **secretagogue**.

secretogranin I *another name for* chromogranin B (*see* **chromogranin**).

secretor any person who secretes water-soluble glycoproteins with A, B, or H blood-group specificities into their mucous secretions, e.g. saliva and gastric juices. Over 80% of humans are secretors, their status being determined by the allelic constitution of a **secretor gene** in their genomes.

secretor gene a gene determining **secretor** phenotype in humans. Whether a person is a secretor or nonsecretor is determined by a pair of allelic genes, *Se* and *se*. Secretors are either *Se*/*Se* or *Se*/*se* while nonsecretors are *se*/*se*. These alleles occur at a different locus from the ABO locus and do not affect the A, B, and H specificities of the red blood cells.

secretory describing a molecule or molecular fragment destined for secretion from a cell, such as secretory protein, polypeptide, etc.

secretory actin-binding protein *abbr.*: SABP; *also called* prolactin-inducible protein; gross cystic disease fluid protein 15; a glycoprotein that has been isolated in several different studies (as the alternative names indicate) but whose function remains unknown. As the prolactin-inducible protein, it was identified as a highly specific and sensitive marker of primary and metastatic breast cancer. Example from human (precursor): database code SABP_HUMAN, 146 amino acids (16.55 kDa).

secretory component *another name for* **secretory piece**.

secretory granule a small subcellular vesicle, surrounded by a single-layered membrane, that is formed from the Golgi apparatus and contains a highly concentrated protein destined for secretion. Secretory granules move towards the periphery of the cell, their membranes fuse with the cell membrane, and their protein load is exteriorized. Processing of the contained protein may take place in secretory granules. *Compare* **zymogen granule**.

secretory piece (*abbr.*: SP) *or* **secretory component** (*abbr.*: Sc) the 58 kDa polypeptide that joins together the two identical monomers comprising the secretory form of **immunoglobulin A**. It has strong affinity for mucus, thus prolonging retention of IgA on mucous surfaces, and may protect this class of immunoglobulin against proteolytic destruction in the digestive tract. *Other names*: T chain; transport piece.

secretory protein I *abbr.*: SP-I; a glycoprotein of the parathyroid gland that is co-secreted *in vitro* with **parathyrin**. It consists

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of at least two homologous glycoproteins of similar size (M_r 72 000 and 70 000), related to chromogranin A (*see* **chromogranin**).

sector any portion of a circle bounded by two radii and the included arc. —**sectoral** *adj.*

sector cell *or* **sector-shaped cell** a cell used in an analytical ultracentrifuge to contain the sample. It is sector-shaped when viewed parallel to the rotation axis. Since the accelerating force is radial, sedimenting molecules move along radii and this cell shape minimizes the collision of sedimenting molecules with the cell walls.

sediment **1** to undergo **sedimentation**. **2** the accumulation of material resulting from sedimentation.

sedimentation the setting of solid particles (or solute) through a liquid (or solution) under the influence of a gravitational or centrifugal field.

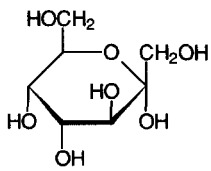
sedimentation coefficient symbol: s; the rate of sedimentation of a particle in an ultracentrifuge or other system. For a particle or solute sedimenting in a system at constant applied field, temperature, and pressure, $s = v/a$, where a is the acceleration of free fall or centrifugation and v is the velocity of sedimentation. In centrifugation $s = v/\omega^2 r$, where ω is the angular velocity in rad s^{-1} and r is the distance of the particle or solute from the axis of rotation. It has the dimensions of time. The sedimentation coefficients of macromolecules and cellular particles are often expressed in **svedbergs**.

sedimentation equilibrium a technique in which compounds of interest are centrifuged for a period sufficiently long for the system to come to equilibrium. The technique has a number of applications. In one, used for molecules that have a density greater than the solvent, centrifugation is carried out at relatively slow speeds so that sedimentation of the molecule is slow enough to be counterbalanced by diffusion. At equilibrium, the concentration is lower at the meniscus and higher at the bottom of the cell, but is unchanging. The relative molecular mass, M_r, of the compound in question, often a protein, can be calculated from the expression:

$$M_r = 2RT \ln(c_2/c_1)/\omega^2(1 - v\rho)(r_2^2 - r_1^2),$$

where R is the gas constant, T is the thermodynamic temperature, v is the specific volume of the component, ρ is the density of the solution, ω is the angular velocity of the rotor, and c_1 and c_2 are the concentrations of the component at distances r_1 and r_2 from the centre of rotation. Ideally, determinations should be done at several concentrations and extrapolated to zero concentration.

sedoheptulose *a nonsystematic name for* D-*altro*-2-heptulose.



α-D-pyranose form

sedoheptulose-bisphosphatase EC 3.1.3.37; a chloroplast enzyme of the **reductive pentose phosphate cycle** that catalyses the reaction:

sedoheptulose 1,7-bisphosphate + H_2O = sedoheptulose 7-phosphate + orthophosphate.

Example from *Arabidopsis thaliana* (precursor): database code S17P_ARATH, 393 amino acids (42.41 kDa).

sedoheptulose 7-phosphate the 7-phosphate ester of **sedoheptulose**; it is a component of the **pentose phosphate pathway**.

Seebeck effect the phenomenon whereby an electromotive force is generated in a circuit containing junctions between dissimilar metals if these junctions are not all at the same temperature. *See* **thermocouple**. *Compare* **Peltier effect**. [After Thomas Johann Seebeck (1770–1831), Estonian-born German physicist.]

segmentation **1** (of an ovum) *see* **cleavage** (def. 3). **2** (of an animal's body) *see* **metamerism**.

segregation *(in genetics)* **1** the separation of homologous genetic elements (i.e. allele pairs) during meiosis in diploid cells. **2** the separation of sister chromatids during mitosis; by extension, the separation of any two independent genetic elements during cell division in prokaryotes. **3** (of plasmids) the partitioning of plasmids into daughter cells at cell division. Naturally occurring plasmids contain a partitioning function, *par*, which ensures correct partitioning into the two daughter cells.

segresome a membrane-bound, cytoplasmic aggregate of a dye, formed either by passage of the dye through the membrane of a pre-existing **phagosome** or **lysosome**, or by some process leading to the *de novo* formation of a membrane around the dye aggregate.

Seitz filter a filtration apparatus that removes microorganisms from a liquid. It formerly consisted of a flat pad of asbestos, or asbestos and cellulose, suitably mounted between the sample container and the receiving flask, filtration being assisted by reducing the pressure in the receiving flask. It has now been superseded by a sintered-glass filter. [After Seitz-Filter-Werke, T. and G. Seitz Gmbh & Co., Bad Kreuznach, Germany.]

selachyl alcohol 3-(octadec-9-enyloxy)-1,2-propanediol; a 1-octadec-9-enyl ether of glycerol, and a hydrolysis product of **ether lipids**.

selected-ion monitoring *or* **mass fragmentography** *or* **molecular fragmentography** a type of **gas chromatography/mass spectrometry** in which the intensities of one or more molecular or fragment ions selected from the mass spectrum of a particular compound are monitored continuously as a means of quantifying that compound.

selectin any of a group of leukocyte surface molecules that act as leukocyte adhesion molecules; they are classed as CD62 in the **CD marker** system. All have **lectin** family carbohydrate-binding domains and EGF-repeats, with four motifs. They are expressed on the surface of platelets and endothelial cells as well as leukocytes. **E selectin** (CD62E), M_r 107–115 000 in various glycosylated forms, is expressed on endothelial cells, being induced by cytokines such as interleukin 1β and tumour necrosis factor α in 3–6 hours. It mediates endothelial cell binding to neutrophils, monocytes, and some memory T cells. Example from human (precursor): database code LEM2_HUMAN, 610 amino acids (66.58 kDa). **L selectin** (*or* lymph node homing receptor; CD62L), M_r 74 000 (on lymphocytes), is constitutively expressed on monocytes, lymphocytes (thymocytes, NK cells), neutrophils, eosinophils, and basophils. It mediates the adherence of lymphocytes, neutrophils, and monocytes to endothelium, including that of lymphocytes to endothelial cells of high endothelial venules in peripheral lymph nodes. It binds to **MadCAM** and CD34. Example from human (precursor): database code LEM1_HUMAN, 372 amino acids (42.14 kDa). **P-selectin** (*or* PADGEM; *abbr. for* platelet activation dependent granule external membrane protein), M_r 140 000, is expressed at the surface of activated platelets and endothelial cells, and is inducible within minutes by thrombin, histamine, or peroxides from α granules of platelets or Weibel–Palade bodies of neutrophils. It mediates the adhesion of neutrophils and monocytes to platelets and endothelial cells. Example from human (precursor): database code LEM3_HUMAN, 830 amino acids (90.74 kDa).

selection *(in microbiology)* a laboratory method in which a mixture of microorganisms is cultured under particular growth conditions that permit only cells with certain characteristics to survive, thereby enabling their isolation.

selection pressure the intensity with which natural selection operates; it is often measured by the change in **gene frequency** per generation due to the effects of natural selection.

selectively labelled indicating an isotopically labelled mol-

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ecule in which the position(s) of the labelling is known, but the number of labelling nuclides at that (those) position(s) is not known; e.g. selectively labelled ethanol is designated as [1,2-^{2}H]CH_3–CH_2–OH, which indicates that some, or all, of the hydrogen atoms on carbon atoms 1 and 2 are ^{2}H atoms.

selective medium a culture medium designed either to encourage or to inhibit the growth of certain types of organisms, especially microorganisms.

selective theory of immunity *or* **elective theory of immunity** any theory that ascribes to antigens a selective function in immunity by which antigens select cells genetically prepared to respond specifically and cause them to multiply and differentiate. They include the **clonal-selection theory** and the **natural-selection theory of immunity**. *Compare* **instructive theory of immunity**.

selenium *symbol*: Se; a metalloid element of group 16 of the (IUPAC) **periodic table**; atomic number 34; relative atomic mass 78.96. Its main oxidation states are –2, +2, +4, and +6, with properties similar to those of sulfur, but more metallic. It occurs in various allotropic forms (grey, red, black); the grey form shows some electrical conductivity, which is enhanced by light, and it is used in 'selenium cells' to measure light intensity. There are several isotopes, the most abundant being selenium-80 (mass 79.916; relative abundance 49.8%); others are selenium-74 (0.9%), selenium-76 (9.0%), selenium-77 (7.6%), selenium-78 (23.5%), and selenium-82 (9.4%). Radioactive isotopes are **selenium-72**, **selenium-73**, **selenium-75**, and **selenium-79**. Selenium is an essential trace element, required for the formation of **selenoproteins**, notably **glutathione peroxidase**. Gut absorption is poor, but selenium deficiency is rare (seen, e.g., in some parts of China with low soil selenium). The most obvious clinical feature of dietary deficiency is myopathy (especially cardiomyopathy). Measurement of red-cell glutathione peroxidase activity gives an index of selenium status.

selenium-72 a radioactive nuclide of selenium, $^{72}_{34}$Se, mass 71.927; it emits gamma radiation (0.046 MeV) and has a half-life of 8.4 days.

selenium-73 a radioactive nuclide of selenium, $^{73}_{34}$Se, mass 72.927; it emits a β^+ particle (1.32 MeV) and gamma radiation (0.361 Mev) and has a half-life of 7.1 h.

selenium-75 a radionuclide of selenium, $^{75}_{34}$Se, mass 74.923; it emits gamma radiation (0.481 MeV) and has a half-life of 118.5 days.

selenium-79 a radionuclide of selenium, $^{79}_{34}$Se, mass 78.918; it emits an electron (β^- particle, 0.16 MeV), no gamma radiation, and has a half-life of 6.5×10^4 years.

selenoamino acid an amino acid in which selenium replaces a sulfur atom; *see* **selenocysteine**, **selenomethionine**.

selenocysteine H–Se–CH_2–$CH(NH_2)$–COOH; an essential component of glutathione peroxidase and some other proteins (*see* **selenoprotein**). For its synthesis, a special tRNA charged with serine responds to a UGA codon. The serine is converted to selenocysteine just before its use on the ribosome. It is assumed that the neighbouring base sequence indicates a special sense for this codon, which is normally a 'stop' codon.

selenomethionine CH_3–Se–$[CH_2]_2$–$CH(NH_2)$–COOH; a selenoamino acid used as an antimetabolite, competing with methionine; it is also found in proteins; *see* **selenoprotein**.

selenoprotein a protein containing selenium, almost invariably as **selenocysteine**, although **selenomethionine** can occur, apparently as a random substitute for methionine. Well-known selenoproteins include the mammalian **glutathione peroxidases** and tetraiodothyronine 5′-deiodinase, and bacterial formate dehydrogenases and glycine reductase.

self **1** the individuality of a person or thing; the totality of components intrinsic to an individual or thing. **2** *(in immunology)* the components of an individual's own tissues that can be distinguished from foreign substances by the individual's immune system, and towards which **immunological tolerance** is shown.

self-absorption the absorption of any emission by the emitting molecules.

self antigen any (potentially) antigenic molecule originating in an individual that is recognized as nonforeign by the individual's immune system, and towards which **immunological tolerance** is normally shown. *See also* **autoimmunity**, **self-tolerance**.

self-assembly the formation of a complex entity from more simple, identical units without intervention from any external agency.

self-assembly doctrine a doctrine elaborated by Caspar and **Klug** to explain the assembly of small viruses and subcellular organelles. It is postulated that the structure assembles as a result of specific binding sites on proteins that interact to form a scaffold on which other components form.

self-catabolite repression **repression** of gene expression by a **catabolite** formed within the same organism.

self-cloning the cloning of a gene within the species from which it was derived, a technique that in some countries attracts less stringent government restrictions than when a gene is cloned in another species, being considered the less hazardous of the two approaches with respect to the genetic environment.

self determinant a **determinant** originating from the tissue of an organism and thus treated as **self** (def. 2) by the immune system of that organism (except in the case of autoimmune pathology; *see* **autoimmunity**).

self-fertilization the union of male and female gametes of the same organism.

self-hybridization hybridization between nucleic acids that exhibit complementarity.

selfing *(in microbiology)* the production of wild-type 'transductants' by infection of an auxotrophic strain with a transducing phage grown on the same auxotroph as the donor.

selfish DNA hypothesis a hypothesis put forward to account for the presence in eukaryotic genomes of large amounts of repetitive DNA (*see* **repetitive sequences**). Because there is no confirmatory evidence that much of such DNA serves any useful purpose for its host, this DNA has been termed **selfish DNA** or **junk DNA**, and is suggested to be a molecular parasite that, over many generations has disseminated itself throughout the genome. If this is true, it remains a mystery why natural selection has not eliminated 'selfish DNA'.

self tolerance the state in which the immune system of any particular individual lacks reactivity against potentially antigenic molecules originating within that individual. Self tolerance develops during perinatal life. *See also* **acquired tolerance**, **autoimmunity**, **immunological tolerance**.

Seliwanoff test a test for ketohexoses based on the production of a red colour when the sample is boiled with a solution of 0.05% w/v resorcinol in 3 M hydrochloric acid. The test relies on the fact that ketoses are dehydrated more rapidly than aldoses to yield furfural products. [After Feodor Feodorowitsch Seliwanoff (1859–1938), Russian chemist.]

SEM *or* **S.E.M.** **1** *abbr. for* standard error of estimate of mean. **2** *abbr. for* scanning electron microscope; *see* **electron microscope**.

sem-5 the gene for Sem-5, sex muscle abnormal protein 5, in *Caenorhabditis elegans*. Sem-5 acts both in vulval induction and sex myoblast migration, and is linked in a signalling chain from tyrosine kinase receptors (e.g. EGF-type Let-23). It contains SH2 and SH3 domains (*see* **SH domain**) characteristic of tyrosine kinase binding proteins. Mutations of the *sem-5* gene block signalling pathways from several tyrosine kinase receptors in the worm. Database code SEM5_CAEEL, 228 amino acids (26.18 kDa).

semantide *or* **semantophoretic molecule** *or* **informational macromolecule** any of the different types of macromolecules that carry the information of the genes or a transcript (or a translation) thereof. The genes themselves are **primary semantides**, messenger RNA molecules are **secondary semantides**, and most polypeptides are **tertiary semantides**.

semantophoretic molecule *an alternative name for* **semantide**.

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semen the fecundating fluid of male higher animals, consisting of spermatozoa suspended in seminal plasma – secretions of the accessory glands.

semenogelin one of two major gel-forming proteins of semen. These proteins have 80% of their amino-acid residues in common, and their genes are localized to the long arm of chromosome 20. They are hydrolysed by a **kallikrein**-like proteinase. Example (precursor) of the predominant human protein of this type, semenogelin 1: database code SEM1_HUMAN, 462 amino acids (52.07 kDa).

semi+ *prefix* **1** half. **2** partial or partially; intermediate.

SEMI *abbr. for* specific endogenous mitotic inhibitor; *see* **chalone**.

semialdehyde any of a class of organic compounds formed by the reduction of one carboxyl group of a dicarboxylic acid to an aldehyde group, as in glutamic semialdehyde.

semiconductor any material, e.g. germanium or silicon, whose electrical conductivity lies between that of conductors and insulators and increases with increasing temperature. Its crystal structure has atomic bonds that allow the conduction of electric current by either positive or negative carriers when the appropriate additives (dopants) are present.

semiconservative replication of DNA *see* **replication of DNA**.

semiconstitutive mutant a mutant in which negative regulation is partially lost, so that a gene is expressed in the absence of inducer, but at a lower level than in the fully constitutive mutation, yet in the presence of inducer the expression reaches the fully constitutive level. *See also* **constitutive mutation**.

semi-micro **1** describing or concerning something moderately small; applied to a scale of operation, an item of equipment, a quantity of material, etc. **2** *(in analytical chemistry) a term originally used to indicate* analysis of amounts of substance in the range 10–100 mg. *Compare* **micro** (def. 1). *See also* **microanalysis**.

seminal **1** **a** pertaining to seed. **b** of, or relating to, semen. **2** (of an experiment, idea, or publication) germinating new concepts; fundamentally original.

seminal plasma the suspending fluid in which semen is ejaculated.

seminalplasmin *another name for* **caltrin**.

semiochemical any chemical substance that delivers a message or signal from one organism to another. The two broad classes into which such substances are divided are known as **pheromones** and allelochemics, depending on whether the information transfer occurs between, respectively, individuals of the same species (intraspecific) or between members of different species (interspecific). *See also* **allomone**, **kairomone**.

semiotics *functioning as sing.* **1** the practice of symptomatology; a term that became obsolescent, but has been reintroduced in connection with CT, NMR, and other imaging techniques. **2** the philosophical theory of signs and symbols, having three branches: syntactics, semantics, and pragmatics.

semipermeable membrane a membrane that allows the passage of only certain solutes, usually small molecules, but is freely permeable to solvent.

semipolar double bond *an alternative name for* **dipolar bond**.

semiquinone any free radical derived from a quinone or quinoid compound by the removal from it of a single hydrogen atom. *Compare* **quinone**.

semisolid medium *(in cell culture)* a medium of consistency between those of a solution and a full gel.

semisynthesis the partial synthesis of a chemical compound, especially a novel substance, by chemical or/and enzymic modification of one isolated from natural sources or produced biotechnologically (e.g. by fermentation). The procedure has been applied with conspicuous success in the manufacture of new pharmaceuticals such as artificial penicillins and cephalosporins. —**semisynthetic** *adj.*

semisystematic name *or* **semitrivial name** *(in organic-chemical nomenclature)* a name of a molecular entity that has only a part of it used in a systematic sense; e.g. (meth)ane, (but)ene, (calci)diol (in each of which only the part of the name outside the parentheses is systematic). Most names in organic chemistry are of this type. *Compare* **systematic name**, **trivial name**.

senescence the process of ageing. —**senescent** *adj.*

senile aged, to a point of severely decreased capability. —**senility** *n.*

senna a preparation of the dried leaves of *Cassia angustifolia* or *C. senna* used as a laxative. It contains glycosides of hydroxyanthracene (sennoside B), which are metabolized to purgative anthraquinones by colonic bacteria.

sense DNA *see* **coding strand**.

sense strand (of duplex DNA) *see* **coding strand**.

sensitivity **1** an index of the ability of any analytical method or other detection procedure to make quantitative determinations at very low levels. **2** *(in metabolic control theory)* the susceptibility of flux through a pathway to change in response to change in the level of one of the component enzymes, expressed quantitatively in terms of the **flux control coefficient**. An alternative meaning arises when an allosteric ligand acts at several points in a pathway, where a plot of the fractional modification in flux versus ligand concentration yields a sigmoidal curve for a positive effector; the sensitivity in this case can be derived from the slope of the sigmoidal curve.

sensitivity coefficient *former name for* **flux control coefficient**.

sensitization *or* **sensitisation** **1** enhanced reactivity to any treatment (such as exposure to an agonist) of any tissue, cell, or molecular system resulting from prior experience or treatment (often by the same agonist). **2** the conditioning of an animal by antigen in such a way that **hypersensitivity** reactions occur on subsequent exposure to the antigen. **3** the attachment of antibody to sheep red blood cells to make them susceptible to lysis by complement in the **complement-fixation test**. Red blood cells treated in such a way are commonly referred to as **sensitized cells**. —**sensitize** *or* **sensitise** *vb.*

sensitizer *or* **sensitiser** *see* **allergen**.

sensor any device that records the level of a substance of interest or under investigation, using physical parameters (heat, conductivity) or chemical methods. Sensors are often applied to continuous monitoring in flow systems; **biosensors** utilize the reactions of enzymes immobilized on a probe and often coupled with a second substrate that yields a coloured or fluorescent product.

sensory transducer any component of bacterial systems involved in signal transduction. An example is the *ntrB*/*ntrC* system, which occurs in several bacteria (the following examples are from *Escherichia coli*). Under nitrogen limitation the product of the *ntrB* gene, NtrB (EC 2.7.1.–), activates NtrC – the *ntrC* gene product – by phosphorylating it; in nitrogen excess it reverses this. Examples: NtrB, database code NTRB_ECOLI, 349 amino acids (38.51 kDa); NtrC, database code NTRC_ECOLI, 469 amino acids (52.19 kDa); NtrC contains an ATP-binding domain that interacts with **sigma factor** σ^{54}. Another instance of a sensory transducer is sensory rhodopsin I transducer from archaebacteria. Example from *Halobacterium halobium*: database code HTRI_HALHA, 536 amino acids (56.61 kDa); this is a typical seven-transmembrane-domain **opsin**-type protein used for sensing light. *See also* ***che***.

separation *(in genetics)* the break-up of a cointegrate into two or more **replicons** of similar sizes. *Compare* **excision**.

Sephacel *proprietary name for* a gel-filtration medium based on **cellulose** cross-linked using **epichlorohydrin** so that a mesh results, the size of the apertures in the mesh being determined by the extent of cross-linking.

Sephacryl *proprietary name for* a gel-filtration medium prepared from allyldextran covalently cross-linked using *N*,*N*-methylene bisacrylamide, to yield a mesh; the size of the apertures in the mesh depend on the degree of cross-linking.

Sephadex *proprietary name for* a gel-filtration medium based on **dextran** cross-linked using **epichlorohydrin** so that a mesh results, the size of the apertures in the mesh being determined by the extent of cross-linking.

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Sepharose *proprietary name for* a gel-filtration medium based on **agarose** cross-linked using **epichlorohydrin** so that a mesh results, the size of the apertures in the mesh being determined by the extent of cross-linking.

septanose the form of any **monosaccharide**, or monosaccharide derivative, in which the molecule contains a ring consisting of six carbon atoms and one oxygen atom. In monosaccharide symbolism the septanose form may be indicated by the suffix *s*; e.g. Glc*s* symbolizes glucoseptanose. *Compare* **furanose**, **heptose**, **pyranose**.

septate divided by, or involving, a **septum** or septa.

septation the process of forming the **septum** that cuts a cell into two at the end of the **cell cycle** in bacteria.

septum **1** *(in anatomy)* a wall of tissue, sheet of cells, or other membrane-like structure that partitions two compartments. **2** a disk of silicone rubber, PTFE, or similar material used in any apparatus to seal an injection port. The needle of a syringe can be punched through the septum for the purpose of injection, and on withdrawal of the needle the elasticity of the septum ensures that the hole reseals.

Sequenase *proprietary name for* a chemically modified T7 DNA polymerase with high **processivity**. It is the usual choice for DNA sequencing by the **chain-termination method**.

sequenator an apparatus for determining the sequence of monomeric residues (e.g. amino acids) in an ordered linear polymer (e.g. an oligopeptide) by repeating a chemical process.

sequence **1** the ordinal arrangement of the constituent parts of a biopolymer, e.g. the order of amino-acid residues in a polypeptide chain or of the nucleotide residues in a polynucleotide chain; the known arrangement of such units in any biopolymer or fragment. **2** any particular segment, occurring in or derived from a biopolymer, having a known order of its constituent parts; a synthetic polymer composed of parts equivalent to those occurring naturally and present in a particular known order. **3** to determine the order of residues in a biopolymer or fragment. —**sequential** *adj.*

sequence compression *see* **band compression**.

sequence homology similarity (often to an indicated degree) of sequences of residues in encoded macromolecules or specified segments of them. The term is often used synonymously with **conservation** (when used of primary structure) if the sequences occur in corresponding locations in specimens of any particular macromolecule obtained from genetically differing sources. Homology is discussed more fully in **Appendix E**.

sequence hypothesis the hypothesis, formulated by F. H. C. **Crick** in 1958, that 'the specificity of a piece of nucleic acid is expressed solely by the sequence of its bases, and that this sequence is a (simple) code for the amino-acid sequence of a particular protein.'

sequence ladder the ladder-like bands of separated components occurring in the chromatographic gel that result from DNA sequencing experiments.

sequencer an apparatus for automatically determining the sequence of monomeric residues in an ordered linear polymer.

sequence rule *or* **Cahn–Ingold–Prelog rule** *or* ***R/S* convention** (of configuration specification) a system for specifying the absolute molecular chirality of a chemical compound. This system considers the sequence of the proton numbers of the atoms directly attached to a chiral centre (*see* **chirality**); if two or more of these atoms have the same proton number, their substituents are then taken into account, the group with substituents of highest proton number taking precedence. When a multiple bond to a substituent is present, the substituent is arbitrarily considered to occur twice, or thrice; an isotope of higher nucleon number takes precedence over one of lower number. The priorities of some common ligands are tabulated in **Appendix G**. For a tetrahedral centre (e.g. a carbon atom) the substituent with the lowest priority is placed away from the observer (behind the chiral atom) with the other three projecting towards the observer; if these three substituents lie in a clockwise (right-handed) array of decreasing priority, then the chiral centre is designated with the stereochemical descriptor *R*, denoting Latin *rectus*, right; if the substituents lie in an anticlockwise (left-handed) array of decreasing priority, then the chiral centre is designated with the stereochemical descriptor *S*, denoting Latin *sinister*, left. For the name of a compound consisting of molecules with a single chiral centre the descriptor *R* or *S*, with a preceding locant if needed, is formed into a prefix by placing it in parentheses and adding a linking hyphen; a racemate with a single chiral centre in its molecules is labelled with the prefix (*RS*)-. When a molecule contains more than one chiral centre the prefix to the name is composed of multiple descriptors, each preceded by an appropriate locant; e.g. (2*R*,3*R*)-2,3-dihydroxybutanedioic acid (= L$_g$-tartaric acid). If only the relative, but not the absolute, configurations of two or more chiral centres in a molecule are known, these centres may be designated with the descriptors *R** and *S** (spoken as *R* star, *S* star), preceded when necessary by appropriate locants, on the arbitrary assumption that the chiral centre first cited (which usually is the one with the lowest locant) has an *R* configuration; for examples, compare the systematic names of **allothreonine** and **threonine**. *See also* **D/L convention**. Extensions of the sequence rule are the ***E/Z* convention**, the **pro-*E*/pro-*Z* convention**, the **pro-*R*/pro-*S* convention** and the ***Re*/*Si* convention**. [After Robert Sidney Cahn (1899–1981), British natural-products chemist, editor, and scientific semanticist, (Sir) Christopher Kelk Ingold (1893–1970), British physical organic chemist, and Vladimir **Prelog**, who jointly developed the system and described it in a series of three papers published in 1951, 1956, and 1966.]

sequence-tagged site *abbr.*: STS; a short, single-copy DNA sequence that characterizes a mapping landmark on the genome. Such sequences provide unambiguous identification of DNA markers generated by the Human Genome Project (*see* **HUGO**). STSs are short segments of DNA of known (and unique) sequence which bind to **YACs**. If two YACs contain the same STS they must overlap. The YACs can be built up into an overlapping series of clones (a **contig**) covering an entire gene.

sequencing the act or process of determining the **sequence** (def. 1) of proteins or nucleic acids. *See* **chain-termination method**, **chemical cleavage method**, **solid-phase technique**.

sequencing by hybridization *see* **SBH**.

sequencing gel a polyacrylamide gel run to resolve oligonucleotides produced in a DNA sequencing procedure. *See* **chain-termination method**, **chemical cleavage method**.

sequential analysis the analysis of a protein or nucleic-acid **sequence** (def. 1).

sequential mechanism an enzyme reaction involving two or more substrates in such a way that all the substrates must be bound to the enzyme to form the central complex before any products can be released. A sequential mechanism may be an **ordered mechanism** or a **random mechanism**.

sequestering agent *see* **chelating agent**.

sequestration **1** the process of removal or separation. **2** *(in chemistry)* the effective removal of ions from solution by **co-ordination** with another kind of ion or molecule to form a firm complex molecule with different properties from the original ion. *Compare* **chelation**. **3** *(in cell biology)* the intracellular enclosing of material in an organelle. —**sequester** *vb.*

Ser *symbol for* a residue of the α-amino acid L-serine (alternative to S).

SER *abbr. for* smooth endoplasmic reticulum (*see* **endoplasmic reticulum**).

sera a plural of **serum**.

SERCA *abbr. for* sarcoplasmic/endoplasmic reticulum **calcium-transporting ATPase**, EC 3.6.1.38; any of a family of Ca^{2+} pump integral membrane protein isoforms of sarcoplasmic or endoplasmic reticulum. They catalyse the hydrolysis of ATP coupled with Ca^{2+} transport. Example from *Drosophila melanogaster*: database code ATCB_DROME, 1002 amino acids (109.47 kDa).

serial dilution a method of achieving dilution of a liquid by se-

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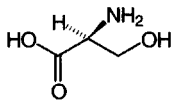
quentially transferring a sample of predetermined volume into another, empty, vessel (usually a tube), which is then made up with diluent to the same total volume as the first. The overall dilution achieved is $(v/s)^x$-fold, where v is the chosen total volume in each tube, s is the size of the sample, and x is the number of times the procedure is repeated.

serinate **1** serine anion; the anion, $HO–CH_2–CH(NH_2)–COO^-$, derived from **serine**. **2** any salt containing serine anion. **3** any ester of serine.

serine *the trivial name for* α-amino-β-hydroxypropionic acid; 2-amino-3-hydroxypropanoic acid; $HO–CH_2–CH(NH_2)–COOH$; a chiral α-amino acid. L-Serine (*symbol*: S *or* Ser), (*S*)-2-amino-3-hydroxypropanoic acid, is a coded amino acid found in peptide linkage in proteins; codon: AGC or AGU; UCA, UCC, UCG, or UCU. In mammals it is a nonessential dietary amino acid and is glucogenic. D-Serine (*symbol*: D-Ser *or* DSer), (*R*)-2-amino-3-hydroxypropanoic acid, in both free and combined forms occurs in silkworms and earthworms; residues of D-serine occur in certain peptide antibiotics, e.g. polymyxins D_1 and D_2. [*Note*: The absolute configuration of D-serine (and hence that at the α-carbon atom of other α-amino acids of the D series) is identical with that of D-glyceraldehyde (and hence with that at the reference carbon atom of other monosaccharides of the D series).]



L-serine

L-serine dehydratase EC 4.2.1.13; *systematic name*: L-serine hydro-lyase (deaminating); *other names*: serine deaminase; L-hydroxyaminoacid dehydratase. An enzyme that catalyses a reaction between L-serine and water to form pyruvate and ammonium ion. It is a pyridoxal-phosphate enzyme. The enzyme for gluconeogenesis from serine in *Escherichia coli* is a 4Fe–4S protein: database code SDHL_ECOLI, 454 amino acids (48.85 kDa).

serine hydroxymethyl transferase *see* **glycine hydroxymethyltransferase**.

serine-like carboxypeptidase *see* **serine endopeptidase**.

serine *C*-palmitoyltransferase EC 2.3.1.50; an enzyme of the pathway for the biosynthesis of **sphingoid** bases. It catalyses the formation of 3-dehydro-D-sphinganine from palmitoyl-CoA and L-serine, releasing CoA and CO_2. Pyridoxal-phosphate is a coenzyme. Example from yeast (long-chain-base biosynthesis protein), two forms: database code LCB1_YEAST, 558 amino acids (62.16 kDa); and database code LCB2_YEAST, 561 amino acids (63.04 kDa).

serine peptidase any enzyme characterized by having a residue of serine (and one of histidine) at the active centre and by being irreversibly inhibited by organic fluorophosphates (which phosphorylate the serine's hydroxyl group). Serine peptidases are of two types: (1) **serine-type carboxypeptidases**, and (2) **serine endopeptidases**, sub-subclass EC 3.4.21. During catalysis by serine peptidases an acyl-enzyme intermediate is formed by esterification of the hydroxyl group of the reactive serine with the carbonyl group of a sensitive peptide bond of the substrate. The serine endopeptidase group includes **chymotrypsin**, most **elastases**, **kallikrein**, **thrombin**, **trypsin**, and a number of microbial proteinases. *See also* **serine-type carboxypeptidase**.

serine/threonine kinase a **protein kinase** that phosphorylates serines or threonines on its target protein.

serine/threonine-specific protein phosphatase EC 3.1.3.16; *recommended name*: phosphoprotein phosphatase; *other names*: protein phosphatase-1; protein phosphatase-2A; protein phosphatase-2B; protein phosphatase-2C. This name includes a group of enzymes that hydrolyse the serine- or threonine-bound phosphate group from many phosphoproteins. Examples from yeast: PP2a-1 catalytic subunit: database code P2A1_YEAST, 369 amino acids (41.89 kDa); PP2a-2 catalytic subunit: database code P2A2_YEAST, 377 amino acids (43.00 kDa).

serine transhydroxymethylase *see* **glycine hydroxymethyltransferase**.

serine-type carboxypeptidase EC 3.4.16.1; this name includes many enzymes that hydrolyse protein with release of a C-terminal amino acid; they have a broad specificity.Examples (3-D structures) from wheat (chains a and b, respectively): database codes NRL_1WHSA, 255 amino acids (28.38 kDa), and NRL_1WHSB, 153 amino acids (17.28 kDa).

serinium serine cation; the cation, $HO–CH_2–CH(NH_3^+)–COOH$, derived from **serine**.

serino+ *prefix* denoting the group, $HO–CH_2–CH(NH–)–COOH$, derived from **serine** by loss of hydrogen from the amino group.

sero+ *comb. form* denoting a connection within or origin in **serum**.

serological pertaining to, or originating in, serum; connected with the study of serum.

serology the study of **serum**; in particular, the immunological phenomena involving circulating antibody that may be observed *in vitro*.

serosa a **serous membrane**, especially the peritoneal covering. — **serosal** *adj.*

serotonergic **1** describing a nerve that is activated by **serotonin**. **2** describing a nerve that acts by the release of serotonin from the nerve endings. *Compare* **adrenergic**, **aminergic**, **cholinergic**, **peptidergic**, **purinergic**.

serotonin 5-hydroxytryptamine (*abbr.*: 5-HT); a monoamine neurotransmitter occurring in the peripheral and central nervous systems, also having hormonal properties; it is also found in mast cells, platelets, brain, and the enterochromaffin cells of the gastrointestinal tract, and is capable of causing vasoconstriction, increased vascular permeability, and contraction of smooth muscle. It is formed from tryptophan, after hydroxylation to 5-hydroxytryptophan, by tryptophan 5-monooxygenase (EC 1.14.16.4) followed by decarboxylation by aromatic-L-amino-acid decarboxylase (EC 4.1.1.28). It is a substrate for **monoamine oxidase**.

serotonin receptor *see* **5-hydroxytryptamine receptor**.

serotransferrin *see* **transferrin**.

serous **1** relating to or resembling **serum** (or similar watery fluid). **2** producing a fluid resembling serum.

serous membrane *or* **serosa** a thin connective-tissue membrane lining certain closed body cavities and reflected over the viscera. The peritoneum of the abdomen, pleura of the chest, and pericardium of the heart are all serous membranes. Each consists of a **parietal layer**, lining the walls of the cavity, and a **visceral layer** covering the organs. The two are continuous, forming a closed sac. *Compare* **mucous membrane**.

serpentine domain any sequence of transmembrane segments of a single polypeptide chain of a membrane protein that traverses the membrane several times, as, e.g., in **seven-transmembrane-domain proteins**.

serpin any of a superfamily of proteins, many of which inhibit serine proteinases and exhibit a high degree of homology with classical serine proteinase inhibitors such as **α_1-antitrypsin** or antithrombin. The superfamily is now considered to extend beyond compounds that are known to be proteinase inhibitors and, based on homology, includes proteins such as **ovalbumin** and **angiotensinogen**, which have no inhibitory function. [From serine proteinase inhibitor.]

Sertoli cell *or* **sustentacular cell** a supporting cell of the mammalian testis that surrounds and nourishes developing sperm cells. [After Enrico Sertoli (1842–1910), Italian histologist.]

serum (*pl.* **sera** *or (esp. US)* **serums**) the liquid extruded after blood has clotted and the clot has retracted (**syneresis** (def. 2)). *Compare* **plasma**.

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serum albumin *or* **plasma albumin** the smallest and most abundant of the plasma proteins; M_r 65 000–68 000 for the bovine form, 69 000 for the human. It is involved in the regulation of osmotic pressure and in the transport of sparingly soluble metabolites. The serum albumins belong to a multigene family of proteins that includes **α-fetoprotein** and **vitamin D binding protein**. Human serum albumin has three homologous domains which assemble to form a heart-shaped molecule. It consists of 28 helices, ranging from five to 31 amino-acid residues each, formed into six subdomains; two each of these subdomains form one of the major domains. There is no beta structure. Bovine (serum) albumin (*abbr.*: BSA) and human (serum) albumin (*abbr.*: HSA) are widely used as standards in protein estimations. These include fatty acids, amino acids (such as tryptophan), steroids, metals (e.g. calcium, copper, and zinc), and hydrophobic drugs. *See also* **albumin**.

serum amyloid P-component *abbr.*: SAP; a precursor of amyloid component P. Amyloid component P is found in basement membranes and is associated with **amyloid** deposits.

serum converting enzyme *a former name for* **angiotensin converting enzyme**.

serum globulin any **serum protein** that is also a **globulin**. An early classification of globulins was according to their mobility on electrophoresis. **Serum albumin** moves the fastest; behind albumin on paper electrophoresis or cellulose acetate strips are two bands known as the α_1- and α_2-globulin bands, followed by a β-globulin band with the γ-globulins forming a diffuse band near the origin. The α_1-globulins include thyroxine-binding protein, transcortin, α_1-glycoprotein, α-lipoprotein, and antitrypsin. The α_2-globulins include haptoglobin, α_2-glycoprotein, macroglobulin and ceruloplasmin. The β-globulins include transferrin, β-lipoprotein and β-glycoprotein. The γ-globulins comprise the immunoglobulins.

serum protein any protein contained in serum; the term is usually applied to those proteins present in high quantities. The most prominent of these is **albumin**, which is present in the normal serum of human adults in the range 34–48 g L^{-1}. *See also* **serum globulin**.

serum response element *abbr.*: SRE; a stretch of DNA that regulates promoters for a group of genes that are activated by addition of serum to cell cultures. Such elements have the consensus sequence CCATATTAGG.

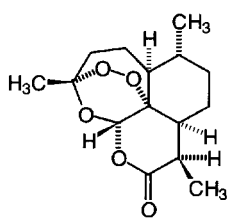
serum spreading factor *see* **vitronectin**.

seryl the acyl group, HO–CH_2–CH(NH_2)–CO–, derived from **serine**.

sesqui+ *comb. form* **1** denoting one-and-a-half times; in a ratio of three parts to two. **2** *(in chemistry)* indicating a compound having one-and-a-half molecular proportions of the specified element group, or unit, either in relation to a second component, as in sesquioxide (e.g. chromium sesquioxide, Co_2O_3), or in relation to a reference compound, as in **sesquiterpene**; it also sometimes denotes a compound intermediate in constitution between two others, as in sesquicarbonate (e.g. sodium sesquicarbonate, $Na_2CO_3{\cdot}NaHCO_3{\cdot}2H_2O$).

sesquiterpene any **terpene** formed from three isoprene units, i.e. having 15 carbon atoms per molecule as compared with a monoterpene which has 10 carbon atoms per molecule and is formed from two isoprene units.

sesquiterpene lactone any sesquiterpene (15 carbon atoms) containing a lactone structure. Several are derived from *Artemisia* spp., including **artemesinin** (qinghaosu) from *A. annua* (qing hao). Qing hao has been used for almost 2000 years as an antimalarial; its mechanism of action is unknown.



artemesinin

sester+ *comb. form* **1** denoting two-and-a-half times; in a ratio of five parts to two or 10 parts to 4. **2** *(in chemistry)* indicating a compound having two-and-a-half molecular proportions of the specified group or unit in relation to a reference compound, as in **sesterterpene**.

sesterterpene any **terpene** formed from five isoprene units, i.e. having 25 carbon atoms per molecule as compared with a monoterpene, which has 10 carbon atoms per molecule and is formed from two isoprene units. An **ophiobolin** is an example.

sev *symbol for sevenless* gene; *see* **Sevenless protein**.

Sevag method a method for removing proteins from nucleic acids during purification of the latter. The proteins are precipitated after repeated denaturation by shaking with a solution of octanol in chloroform.

Sevenless protein *abbr.*: Sev; a protein, encoded by the *sevenless* (*sev*) gene, that is part of a system for differentiation of R7 photoreceptors in *Drosophila*. Sev is a receptor for an extracellular signal; it has **tyrosine kinase** activity and belongs to the family of insulin receptors. Sev has a ligand, **Boss**, the product of the *bride of sevenless* (*boss*) gene; it is expressed by R8 photoreceptor cells and internalized (as a transmembrane protein) in a Sev-dependent manner. Examples, Sev: database code 7LES-DROME, 2554 amino acids (286.79 kDa); Boss: database code BOSS_DROME, 896 amino acids (99.81 kDa).

seven-minute phosphate *see* **labile phosphate**.

seven-transmembrane-domain protein *or* **seven-transmembrane-segment protein** *or* **seven-transmembrane-helix protein** a type of receptor protein that contains, in a single polypeptide chain, seven hydrophobic domains that traverse the lipid bilayer. This structural characteristic is typically used to describe the structures of receptors that couple to effector systems through **G-proteins**. These are also sometimes referred to as serpentine receptors. The structures of only a few membrane proteins have been determined at high resolution, and this structural characteristic has been attributed to other proteins mainly on the basis of sequence comparison. Thus, for the majority of proteins, the name 'seven-transmembrane-domain protein' is a tentative one. The suggestion that the transmembrane domains are helical is even more tentative.

seven-up a receptor required for photoreceptor cells during eye development. It is a **zinc-finger** DNA-binding protein with two forms (1 and 2) generated by alternative splicing. Example (type 1) from *Drosophila melanogaster*: database code 7UP1_DROME, 543 amino acids (57.92 kDa).

sex chromatin a condensed mass of **chromatin** that represents an inactivated X chromosome. In mammalian nuclei, each X chromosome apart from the activated one forms a sex chromatin body or **Barr body**.

sex chromosome a chromosome involved in sex determination. In many species, these are the **X chromosome** and **Y chromosome**. They are distinguished from the **autosomes** i.e. all the other chromosomes of that species. In some species, however, e.g. fish of the genus ***Xiphophorus***, sex determinants are spread over a number of chromosomes.

sex determination the specification of the sex of an individual organism by genes. In many animal species, these genes are located on the **X chromosome** and the **Y chromosome**. Their effects are manifested as a result of secretion of **androgens** and **estrogens**.

sex factor *or* **fertility factor** *or* **F factor** *or* **F agent** an episomal genetic element (*see* **episome**) in bacteria that enables the cell to act as a genetic donor. Cells of such donor strains are able to form stable unions with cells devoid of such factors and to transfer to them extrachromosomal material, including the sex factor, and sometimes segments of bacterial chromosomes (*see* **conjugation** (def. 4)). The **F plasmid** is the prototypical sex factor, responsible for conjugation in certain strains of *Escherichia coli*.

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sex hormone any steroid hormone that is responsible for controlling sexual characteristics and reproductive function. **Estrogens** and **progesterone** are the female sex hormones, while **androgens** are the male sex hormones. They are produced mainly by the ovaries or testes, with contributions from the adrenals and placenta.

sex linkage a special type of gene linkage occurring when a gene producing a certain phenotype (often unrelated to primary or secondary sexual characters) is located on a **sex chromosome**. Such a gene, or the character it determines, is said to be **sex linked**. One consequence of a mutation of genes on the X chromosome is that they may often be apparent only in male offspring, which have only one X chromosome. The mutation may be masked in the female because of the presence of a second, unaffected X chromosome.

sexual conjugation *see* ***conjugation*** (def. 4).

S-form *abbr. for* smooth form; describing bacterial colonies with a **smooth** appearance. *Compare* **R form** (def. 2).

SGF *abbr. for* skeletal growth factor.

SGOT *abbr. for* serum glutamic–oxaloacetic transaminase (name not now recommended; *see* **aspartate transaminase**).

SGPT *abbr. for* serum glutamic–pyruvic transaminase (name not now recommended; *see* **alanine transaminase**).

shadow casting a procedure used in the preparation of specimens for electron microscopic examination. The specimen is placed in a vacuum and a heavy metal is applied by evaporation – the metal is evaporated with an electrically heated tungsten filament. In high vacuum the metal atoms travel in straight lines and so, if evaporation is from an acute angle, metal will condense on only one side of the features of the specimen leading to variations in electron-density over the specimen, creating a 'shadow' effect.

sham operated describing a control procedure in which all the operations employed in a surgical technique are imitated with the exception of the experimental lesion that is the subject of study.

Shardinger enzyme *see* **xanthine oxidase**.

shark's tooth comb a plastic device for creating wells in an electrophoretic gel. It is shaped like a comb with the teeth coming to a point.

Sharp, Phillip Allen (1944–), US molecular biologist; Nobel Laureate in Physiology or Medicine (1993) jointly with R. J. Roberts 'for their discovery of split genes'.

Sharples super centrifuge a, now superseded, efficient centrifuge with a flow-through rotor in which the sedimentation path was short. It is used for harvesting bacteria, blood cells, etc. The version powered with an electric motor turned at 21 000–23 000 rpm while the air-turbine-driven version turned at 50 000 rpm. The instruments of this type have been superseded by others that can operate continuous flow rotors.

SHC a gene family that was identified by screening cDNA libraries for genes encoding SH2-containing proteins (*see* **SH domain**). The mammalian gene encodes two overlapping, widely expressed proteins with a C-terminal SH2 domain that binds activated growth factor receptors, and which are phosphorylated on tyrosine in growth factor activated cells. These Shc proteins are transforming when overexpressed in fibroblasts. Phosphorylated Shc forms a complex with **Grb2**, and may form a link between certain tyrosine kinases and the Grb2/Ras signalling pathway. Example of gene product from human: database code SHC_HUMAN, 473 amino acids (51.61 kDa).

SH domain *abbr. for* Src homology domain; the **SH2 domain** is a protein module consisting of about 100 residues found in many proteins involved in signal transduction. Apart from Src, which contains the prototype SH2 domain (*see* ***src***), these include among many others phospholipase C, products of proto-oncogenes such as ***ABL***, ***FYN***, and ***FGR***, GTPase-activating protein, and protein tyrosine phosphatases. The SH2 domain has also been found in structural proteins such as **fodrin**. One function of the domain is to bind to the autophosphorylated site of growth factor receptors, e.g. PDGF and EGF receptors. Proteins with SH2 domains are frequently found also to have SH3 domains. The **SH3 domain** is composed of approximately 50 amino acids and was originally identified in Src, but has since been found within a number of other proteins. SH3 domains mediate protein–protein interactions through their ability to recognize and bind proteins containing specific amino-acid sequences rich in proline and hydrophobic residues. To date, there are known to be at least two general classes of ligand to which SH3 domains can bind: class I, which comprises proteins containing the consensus sequence PXLPPZP; and class II, with the sequence XPPLPXR (where X is any amino acid and Z appears to be a residue specific to the type of SH3 domain involved). Given the nature of the proteins possessing SH3 domains and SH3-binding domains, it is clear that the protein interactions mediated by these motifs are important to the operation and maintenance of cytoskeletal architecture and intracellular signalling pathways.

shear **1** to disrupt or fracture (an entity) using forces acting parallel to a plane, rather than perpendicularly, as with tensile or compressive forces. For example, shear forces can be used to disrupt DNA or other macromolecules by enclosing the molecules between two closely applied plane surfaces moving rapidly in opposite directions. Homogenization techniques depend on shear forces. **2** the deformation or fracture produced by such forces.

shear gradient *see* **viscosity**.

shear rate *see* **viscosity**.

shear stress *see* **viscosity**.

shikalkin the racemic mixture of **alkannin** and its (+)(*R*) enantiomer, shikonin.

shikimate the anion of shikimic acid; [–]3α,4α,5β-trihydroxy-1-cyclohexene-1-carboxylic acid; (3*R*,4*S*,5*R*)-trihydroxy-1-cyclohexenecarboxylic acid; an important intermediate, in microorganisms and plants, in the pathway for the synthesis of phenylalanine, tyrosine, tryptophan, and many other substances (e.g. tocopherol, vitamin K, folic acid, ubiquinone, enterobactin, and some antibiotics); this is known as the **shikimate pathway**. The enzyme **3-phosphoshikimate 1-carboxyvinyltransferase** (EPSP synthase) in higher plants is specifically inhibited by the compound **glyphosate**, which inhibits growth and can thus be used as an effective and readily degraded broad-spectrum herbicide. Shikimic acid was first isolated from the plant *Illicium religiosum* (star anise) in 1885. The name is derived from the Japanese name for this plant, *shikimi-no-ki*. *See also* **shikimate kinase**.

shikimate 5-dehydrogenase EC 1.1.1.25; *systematic name* shikimate: NADP+ 5-oxidoreductase; an enzyme of the **shikimate pathway** that catalyses the reduction by NADPH of 3-dehydroshikimate to shikimate with formation of $NADP^+$. The description of the enzyme as a 5-dehydrogenase derives from the older numbering system for shikimate. With the now-accepted chemical numbering, it is in fact a 3-dehydrogenase. *See also* **pentafunctional arom polypeptide**.

shikimate kinase EC 2.7.1.71; *systematic name*: ATP:shikimate 3-phosphotransferase; an enzyme of the **shikimate pathway** that catalyses the phosphorylation by ATP of shikimate to shikimate 3-phosphate with formation of ADP. The product, shikimate 3-phosphate, is the precursor of 5-*enol*pyruvylshikimate 3-phosphate (5-*O*-(1-carboxyvinyl)-3-phosphoshikimate) from which **chorismate** is formed. Example, shikimate kinase I from *Escherichia coli*: database code AROK_ECOLI, 172 amino acids (19.39 kDa). *See* **pentafunctional arom polypetide** for another example. *See also* **shikimate**.

shikimate pathway the 'classical' shikimate pathway in plants and microorganisms led to the production of the aromatic amino acids (phenylalanine, tyrosine, tryptophan) from carbohydrate precursors, with a requirement for **chorismate** as well as **shikimate**. Chorismate was regarded as a (single) branch point, being converted to phenylalanine and tyrosine via prephenate (*see also* **arogenate**) and to tryptophan via anthranilate. Chorismate can also be converted to ubiquinones,

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plastoquinones, and tocopherols. Moreover, on isomerization it yields isochorismate, from which are derived many naphthoquinones (including the vitamins K), 3-carboxy aromatic amino acids, salicylate, and dihydroxybenzoate (for enterobactin formation). Certain non-aromatic cyclohexane compounds are produced from shikimate itself. The pathway is now recognized to contain multiple branch points at many (possibly all) of the pathway intermediates, and has been termed a 'metabolic tree with many branches'. The carbohydrate precursors are phospho*enol*pyruvate and D-erythrose 4-phosphate; they yield 2-dehydro-3-deoxy-D-*arabino*-heptonate 7-phosphate (I, more commonly termed 3-deoxy-D-*arabino*-heptulosonate 7-phosphate, *abbr.*: DAHP) by action of EC 4.1.2.15, 2-dehydro-3-deoxyphosphoheptonate aldolase (DAHP synthase). I is converted to 3-dehydroquinate (II) by 3-dehydroquinate synthase, EC 4.6.1.3, and II is then converted to 3-dehydroshikimate (III) by 3-dehydroshikimate dehydratase, EC 4.2.1.10. Shikimate is then formed from III by **shikimate 5-dehydrogenase**, EC 1.1.1.25, and converted to shikimate 3-phosphate (IV) by **shikimate kinase**, EC 2.7.1.71. Phospho*enol*pyruvate is used again to convert IV to 5-*enol*pyruvylshikimate 3-phosphate (V, *abbr.*: EPSP) by 3-phosphoshikimate 1-carboxyvinyltransferase, EC 2.5.1.19, and V yields chorismate (VI) by action of **chorismate synthase**, EC 4.6.1.4. Chorismate leads to prephenate by action of **chorismate mutase**, EC 5.4.99.5, and in another branching undergoes isomerization by isochorismate synthase, EC 5.4.99.6, to form isochorismate. Organization of the various enzymatic activities varies considerably in plants, bacteria, yeasts, and other fungi. In yeasts and other fungi, and also in *Euglena gracilis*, the conversion of DAHP to EPSP requires a complex pentafunctional polypeptide specified by the *arom* gene cluster (*see* **pentafuctional arom polypeptide**).

shikonin the (+)-(*R*) enantiomer of **alkannin**.

Shine–Dalgarno sequence a sequence for the formation of the correct preinitiation complex between a 30S ribosomal subunit and a messenger RNA (mRNA) molecule. It is suggested that a seven-nucleotide, pyrimidine-rich sequence near the 3′ terminus of 16S (prokaryotic) or 18S eukaryote ribosomal RNA, found in many organisms, can form base pairs with a complementary three- to seven-nucleotide, purine-rich sequence (the Shine–Dalgarno sequence) preceding the initiation codon in many mRNA molecules, thereby allowing the initiating ribosomal subunit to bind the mRNA so as to discriminate between many AUG or GUG (i.e. initiation) triplets and to select only the one at the beginning of a cistron. [After John Shine (1946–) and Lynn Dalgarno (1935–).]

shockate the preparation that is obtained when (bacterial) cells are suspended in an osmotically stabilizing medium and lysed by osmotic shocking through the sudden addition of water, followed by immediate centrifugation.

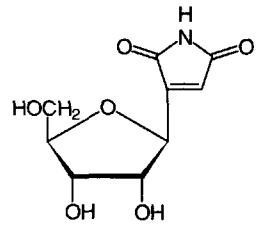
short-chain describing an aliphatic compound of any type with a chain length of less than 10 carbons.

short-patch repair a type of **excision repair** of DNA in which the average size of excised DNA is about 20 nucleotides. It contrasts with **very-short-patch repair**, which deals with mismatches between specific bases, and **long-patch repair**, in which relatively long stretches of DNA are involved, mostly about 1500 nucleotides long, but in some cases up to 9000 nucleotides or more. *See also* **DNA repair enzyme**, ***uvr***.

shotgun cloning a method, first used for cloning an entire genome, in which the DNA is randomly broken into fragments of approximately the average size of genes. The fragments are then cloned into suitable vectors, to give a **genome library**.

shotgun collection *see* **genomic library**.

showdomycin 2-(β-D-ribofuranosyl)-maleimide; an antibiotic produced by *Streptomyces showdoensis* and active against a number of Gram-positive bacteria. It is sometimes used in biochemical studies as a thiol-reactive agent. *Compare* ***N*-ethylmaleimide**.



shuttle *(sometimes)* an intracellular metabolic cycle concerned in the transfer of, e.g., reducing equivalents or carbon chains across membranes. Different carriers operate each way across the membrane. Examples include the **3-hydroxybutyrate cycle**, the **glycerol-3-phosphate cycle**, and the **malate–aspartate cycle**.

shuttle vector a DNA molecule, e.g. a plasmid, that is able to replicate in two different host organisms and can therefore be used to 'shuttle' or convey genes from one to the other.

shuttle vesicle an endocytotic vesicle that transfers proteins across an epithelial cell from one face to another e.g. from the sinusoidal to the bile-canalicular face of a hepatocyte.

sI *symbol for* a residue of the ribonucleoside thioinosine; mercaptopurine ribonucleoside (alternative to Sno).

Si *symbol for* silicon.

Si- *stereochemical descriptor* denoting *sinister* (i.e. counterclockwise, or 'left-handed') configuration of face of a trigonal atom. *See* ***Re/Si* convention**.

SI *abbr. for* Système International (d'Unités); International System (of Units); a rationalized coherent system of metric units, in which the magnitude of any physical quantity may be expressed, that is recommended for use by scientists throughout the world. The system is founded on seven **SI base units**: **ampere**, **candela**, **kelvin**, **kilogram**, **metre**, **mole**, and **second**. There are also 21 **SI derived units**, which are expressed in terms of the base units, and two **SI supplementary units**, **radian** and **steradian**, which are now regarded as dimensionless derived units. A series of prefixes signify decimal multiples and submultiples of any SI unit.

Sia *symbol for* the sialoyl group.

sial+ *a variant of* **sialo+** (before a vowel).

sialagogue *or* **sialogogue** any agent that stimulates the flow of saliva. —**sialagogic** *or* **sialogogic** *adj.*

sialate the anion of **sialic acid**.

sialic of, or relating to, saliva or a salivary gland.

sialic acid any of the *N*- or *O*-substituted derivatives of **neuraminic acid** found as components of complex carbohydrates, e.g. *N*-acetylneuraminic acid (5-(acetylamino)-3,5-dideoxy-D-*glycero*-D-*galacto*-non-2-ulosonic acid, (*abbr.*: Neu5Ac; *see also* **NeuNAc**). Linkage of sialic acids is through C-2 to monosaccharides at the ends of glycosylation chains of glycolipids and glycoproteins. Neu5Ac can also be linked at its C-8 and C-9 hydroxyl groups to another Neu5Ac residue, often forming multiple repeats as in mammalian **NCAM**. Hydroxyl groups at C-4, -7, -8, and -9 can be *O*-acylated (*see also* **NeuOAc**). Other common derivatives are *N*-glycoloylneuraminic acid (in mammals, but not normally in humans; *abbr.*: NeuGc), and N-**ketodeoxyoctanooylneuraminic acid** (e.g. in bacteria).

sialidase EC 3.2.1.18; *recommended name*: exo-α-sialidase; *former name*: neuraminidase; a glycosidase enzyme that hydrolyses 2,3-, 2,6-, and 2,8-glucosidic linkages joining terminal nonreducing *N*- or *O*-acylneuraminyl residues to galactose, *N*-acetylhexosamine, or *N*- or *O*-acylated neuraminyl residues in oligosaccharides, glycoproteins, or glycolipids. Example from *Clostridium perfringens*: database code NANH_CLOPE, 382 amino acids (42.81 kDa).

sialidosis *another name for* **mucolipidosis** I.

sialo- *or (before a vowel)* **sial+** *comb. form* **1** of, or relating to, saliva or a salivary gland; sialic. **2** denoting the presence in a

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compound of one or more residues of sialic acid. *Compare* **asialo+**.

sialoadhesin a macrophage-restricted sialic-acid-dependent glycoprotein receptor of several forms. It contains 17 immunoglobulin-like domains. It is an adhesion molecule that recognizes oligosaccharides terminating in NeuAc(α2-3)Gal in N-linked and O-linked glycans. Example, 16-domain form from the mouse: database code MMSIAL1, 1598 amino acids (172.68 kDa).

sialogogue *a variant spelling of* **sialagogue**.

sialosyl the glycosyl group derived by removal of the exomeric hydroxyl group from sialic acid or sialate.

sialoyl the acyl group derived from sialic acid by removing the hydroxyl group from its carboxyl group.

sickle cell an abnormal red blood cell obtained from an individual exhibiting **sickle-cell anemia**. At low oxygen tensions such cells adopt a crescent shape reminiscent of the blade of a sickle. The defect originates in a mutation leading to replacement of Glu by Val at position 6 in the hemoglobin β chain. In its deoxygenated state the hemoglobin forms long rodlike helical fibres, which cause the deformation of the red cells because the β6 Val can pack into a pocket at the EF corner (between helices E and F) of another β chain, a pocket which is lost in conformational changes resulting from oxygenation. Sickling can also result from β121 Glu → Lys replacement, a site that lies close to β6.

sickle-cell anemia an inherited disease of humans arising in individuals homozygous for a mutation resulting in replacement of Glu by Val at position 6 of the hemoglobin β chain. It is particularly common in populations indigenous to or orginating from subtropical areas, including the Mediterranean region, parts of Saudi Arabia and India, and in those of African origin. The resultant abnormal red blood cells, called **sickle cells**, are removed from the circulation, leading to anemia. There is no satisfactory treatment, and early death often results. Less serious consequences occur in heterozygotes i.e. individuals with **sickle-cell trait**; these survive longer and benefit from greater resistance against the malaria parasite, which is adversely affected by sickle-cell trait during the red-cell phase of its life cycle. This results from the fact that, when the heterozygous sickle cells pass through capilliaries, they sickle, causing them to lose K^+ and killing the malaria parasite, which needs high levels of K^+. *See also* **glucose-6-phosphate dehydrogenase**.

side-by-side model *abbr.*: SBS model *or* SBS; a model of duplex DNA consisting of an alternating arrangement of right-handed and left-handed segments of duplex DNA, or other double-stranded polynucleotide, with five base pairs per segment. This produces a structure similar to the **Watson–Crick model of DNA** except that the two antiparallel strands are side by side rather than intertwined in a double helix.

side chain **1** any part of an organic molecule based on an aliphatic carbon chain that can be regarded as branching from a main chain. **2** the part of an amino acid that extends from the α-carbon atom and is unique for that amino acid.

sideramine one of the two main categories of **siderochrome**. *See also* **sideromycin**.

siderochrome *or* **siderophore** *or* **ironophore** any of various low-molecular-mass Fe(III)-chelating substances elaborated by aerobic or facultatively anaerobic microorganisms, especially when growing in iron-deficient media. Fe^{3+}-siderochrome complexes have very high stability constants (10^{30}–10^{50} $dm^3\ mol^{-1}$). They are taken up by specific transport systems in the microorganisms; subsequent intracellular release of iron requires enzymic action. A siderochrome is thus an iron **ionophore**. Siderochromes are of two main categories, one or both of which may be formed by any particular organism: (1) catechol derivatives, e.g. **enterobactin**; and (2) hydroxamic acid derivatives (or **sideramines**), e.g. **mycobactin** (*see also* **ferrichrome**). It is curious that the transport systems for ferrichrome or ferric enterobactin in certain strains of bacteria appear to be identical with the membrane receptors for colicin M or B respectively (*see* **collcin**), and in the former case for the antibiotic albomycin and various phages as well.

sideromycin any of a class of iron-containing antibiotic substances elaborated by certain actinomycetes. They are structurally related to sideramines (*see* **siderochrome**), by which their antibiotic action can be antagonized.

siderophage *an alternative name for* **siderophore D**.

siderophilin *an alternative name for* serotransferrin, serum **transferrin**.

siderophore **1** *or* **siderophage** a macrophage containing granules of **hemosiderin**. **2** *an alternative name for* **siderochrome**.

siderosome a membrane-bound organelle found in spleen macrophages and containing aggregates of **hemosiderin**. Siderosomes may be derived from **lysosomes**.

siemens *symbol*: S; the SI derived unit of **electric conductance**, defined as the electric conductance between two points on an electric conductor when an electric potential difference of one volt causes an electric current of one ampere to flow; i.e. 1 S = 1 Ω^{-1}. It was formerly called the **mho** or the reciprocal ohm. [After (Ernst) Werner von Siemens (1816–92),German electrical engineer, industrialist, inventor, and metrologist.]

sievert *symbol*: Sv; **1** the SI derived unit of (radiation) **dose equivalent**, equal to one joule per kilogram of living tissue; i.e. 1 Sv = 1 J kg^{-1}. Also, 1 Sv = 100 rem. *Compare* **gray**. **2** *or* **intensity millicurie** an obsolete non-SI unit of intensity of gamma radiation, numerically equal to 8.4 röntgens per hour. [After Rolf Maximillian Sievert (1896–1966), Swedish radiation physicist.]

sievorptive chromatography a form of **chromatography** in which absorption chromatography and molecular-sieve chromatography are combined within a single separative system.

***Si*-face** (of an atom or molecule) *see* ***Re/Si* convention**.

SIF cell *abbr. for* small intensely fluorescent cell.

sigma *symbol*: σ (lower case) *or* Σ (upper case); the eighteenth letter of the Greek alphabet. For uses *see* **Appendix A**.

sigma bond *see* **orbital**.

sigma factor an **RNA polymerase** initiation factor occurring in bacteria; a protein that promotes attachment of the RNA polymerase, of which it is a subunit, to specific initiation sites and is then released. The main sigma factor of *Escherichia coli* is σ^{70}: database code RP70_ECOLI, 613 amino acids (70.18 kDa). An unrelated family is σ^{54} (four motifs), with associated regulatory proteins; members of this are specific to certain operons; example from *E. coli*: database code RP54_ECOLI, 477 amino acids (53.93 kDa). Other sigma factors are involved in response to heat shock and respiratory stress; examples (*E. coli*), σ^E: database code RPOE_ECOLI, 191 amino acids (21.67 kDa); and σ^{32}: database code RP32_ECOLI, 284 amino acids (32.43 kDa). Major switches in transcriptional control in bacteria, e.g. sporulation in bacilli, and transcriptional control in certain phages, involve modification to or replacement of sigma factors.

sigma orbital *see* **orbital**.

sigma receptor any of a class of receptors formerly regarded as opioid receptors but now generally regarded as nonopioid receptors because morphine has a very low affinity for them, and naloxone, the classical opioid antagonist, does not block the action of morphine. They are noted for their activation by powerful psychotomimetic drugs, e.g. **phencyclidine**. These receptors appear to mediate disorientated and depersonalized feelings.

sigma subunit a component of bacterial RNA polymerase; *see* **sigma factor**.

sigmoid *or* **sigmoidal** S-shaped; especially as in a sigmoid flexure (e.g. of the large intestine); or a sigmoid plot, i.e. one similar to a skewed letter S, that is with slope increasing initially slowly, progressively increasing more rapidly, and then decreasing towards a plateau. —**sigmoidicity** *n.*

sigmoid kinetics *(in enzymology)* a type of kinetics of en-

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zyme-catalysed reactions characterized by a sigmoid plot of rate versus substrate concentration. Such kinetics are characteristic of **allosteric** enzymes, in that progressive activation occurs with increasing substrate concentration due to **cooperativity** in binding of substrate. The presence of allosteric modifiers will alter the inflection of the curve, activators shifting it towards that found in Michaelis–Menten kinetics (*see* **Michaelis kinetics**).

signal **1** any variable property or parameter that serves to convey information. **2** the message potentially to be transmitted by any agonist interacting with a cell membrane receptor. **3** a **signal peptide**.

signalase *see* **signal peptidase**.

signal averaging a method used to improve **signal-to-noise ratios**, particularly in spectroscopy, by summing repeated scans of the information. The signals are thereby reinforced while the background noise tends to average out.

signal hypothesis a model proposed for the synthesis of secretory proteins on ribosomes bound to the rough **endoplasmic reticulum**. In 1971 the US cytologist Gunter Blobel (1936–) and the US cell biologist David Domingo Sabatini (1931–) suggested that secretory proteins would have a common sequence of amino-acid residues near the N terminus of the nascent chains and that the peptide, or a modification of it, would then be recognized by a factor mediating the binding to the membrane. César **Milstein** and coworkers in 1972 proposed from experiments in which immunoglobulin light chain mRNA was translated in a reticulocyte lysate system, that light chains are initially synthesized as a precursor of slightly higher molecular weight, which is subsequently converted into the authentic product. From these experiments they proposed, independently of Blobel and Sabatini, that a short peptide at the N terminus of a precursor protein would be a simple way to provide a signal to ensure that secretory proteins were synthesized on membrane-bound ribosomes. This hypothesis has been largely substantiated (*see* **signal peptidase**, **signal peptide**, **signal recognition particle**).

signalling molecule any extracellular or intracellular molecule, e.g. **hormone**, **cytokine**, or **second messenger**, that cues the response of a cell to the behaviour of other cells or objects in its environment.

signal peptidase any of a group of endopeptidases that remove the **signal peptide** after insertion of membrane proteins into the membrane. In prokaryotes there are two types: **1** signal peptidase I, EC 3.4.99.36; *recommended name*: leader peptidase; *other name*: prelipoprotein signal peptidase; an endopeptidase that cleaves N-terminal signal peptides from secreted proteins and periplasmic membrane proteins. It is a protein of the inner membrane with a single transmembrane domain. Example from *Salmonella typhimurium*: database code LEP_SALTY, 324 amino acids (35.78 kDa). **2** signal peptidase II, EC 3.4.99.35; *recommended name*: premurein-leader peptidase; an endopeptidase that selectively cleaves the signal peptide from bacterial membrane lipoproteins, hydrolysing the protein on the N-terminal side of a specific Cys residue. Example from *Haemophilus influenzae*: LSPA_HAEIN, 171 amino acids (19.36 kDa). In eukaryotes, signal peptidases, EC 3.4.–.–, are endoplasmic integral membrane proteins with five subunits, numbered according to the approximate M_r, SPC25, SPC22/23, SPC21, SPC18 and SPC12. Example, SPC21 from *Canis familiaris*: database code SPC3_CANFA, 191 amino acids (21.47 kDa).

signal peptidase II *see* **premurein-leader peptidase**.

signal peptide *or* **leader peptide** any sequence of amino-acid residues which when linked to a newly synthesized protein directs the protein to a location among the organelles of a eukaryotic cell and from the cytoplasm to the periplasmic space of prokaryotic cells. The term was originally applied to the N-terminal linked peptide that is responsible for the attachment of ribosomes which translate the mRNA for secretory proteins to the endoplasmic reticulum. Such peptides usually comprise 20–30 amino-acid residues and are characterized by a central region of hydrophobic amino acids preceded by one or more basic amino-acid residues. An interesting feature is that at the junction of the signal peptide and the mature protein there is no consensus sequence of amino-acid residues, so the basis for the specificity of the protease at this position remains unclear (*see* **signal peptidase**). The term signal peptide is now more generally applied to any peptide that is responsible for the location of a newly synthesized protein within the organelles of eukaryotic cells (*see* **protein kinesis**). Thus it applies to the mitochondrial proteins synthesized in the cytoplasm, nuclear proteins and luminal proteins that are retained within the cisternae of the endoplasmic reticulum. In addition to the signal peptides described, which may be located either at the N terminus or C terminus of the nascent protein and which are subsequently cleaved, single-spanning membrane proteins also contain a signal sequence within the protein known as a **stop-transfer sequence**. This serves to anchor the protein within the membrane. The orientation of the protein within the membrane may be either type I or type II depending on whether the N terminus of the resulting protein is extracytoplasmic (type I) or cytoplasmic (type II). *See also* **signal recognition particle**.

signal recognition particle *abbr.*: SRP; a ribonucleoprotein particle of 325 kDa composed of a 7S (300 nucleotide) RNA molecule and a complex of six different polypeptides. This binds both to the N-terminal signal peptide for proteins destined for the endoplasmic reticulum as they emerge from the large ribosomal subunit and also to the ribosome. This binding arrests further translation thereby preventing the proteins from being released into the cytosol. The SRP–ribosome complex then diffuses to the endoplasmic reticulum where it is bound to the **signal recognition particle receptor**, which allows resumption of protein synthesis and facilitates the passage of the growing polypeptide chain through the **translocon**. Through a process involving GTP hydrolysis, the SRP–SRP receptor complex dissociates and SRP returns to the cytosol. Of the six polypeptides of SRP the 54 kDa subunit (SRP54) is the central player. It contains an N-terminal GTPase domain and a C-terminal domain that binds directly to the signal peptide and the SRP RNA.

signal recognition particle receptor *abbr.*: SRP receptor; a transmembrane heterodimeric protein (α subunit, 69 kDa; β subunit, 30 kDa), also known as **docking protein**, located in the membrane of the rough endoplasmic reticulum. Both subunits contain GTPase domains with which **signal recognition particle** interacts. In the presence of GTP and SRP receptor, SRP is released from the ribosome–nascent chain complex. Example, α subunit (dog): database code SSRA_CANFA, 286 amino acids (31.94 kDa). The α subunits have an unusual charge distribution with a highly negatively charged N-terminus and a highly positively charged but phosphorylated cytoplasmic tail (C terminus). *See also* **signal peptide**, **signal recognition particle**.

signal-to-noise ratio the proportional difference between the average level of values observed for a specific property under investigation (signal) measured against the average of nonspecific values (noise) in any record. *See also* **signal averaging**.

signal transduction the transfer of a signal from the outside to the inside of a cell by means other than the introduction of the signal molecule itself into the cell. Typically, interaction of the extracellular signal – a hormone, growth factor, or other agonist – with a specific membrane receptor leads to synthesis within the cell of one or more **second messengers**, or to activation of other downstream cascades, e.g. by phosphorylation of proteins.

signature *an alternative term for* **motif** (in protein sequences); the word is used in the **PRINTS** database. *See* **Appendix E**.

significant *(in statistics)* reaching a degree of **probability** that experimental values lie on a distribution different from that of control values, such that the investigator will conclude that experimental and control samples differ, using tests such as Student's *t*-test or the chi-square test. The degree of probabil-

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ity that will be accepted as indicating a significant difference depends on the type of investigation being conducted. If the tests indicate that the probability that the results are due to chance is ≥5% (for biological or medical studies) or ≤1% or, in some cases, ≤0.1% (for biochemical studies), differences are considered significant. —**significance** *n.*

silane **1** monosilane; silicon tetrahydride; SiH_4; the silicon-containing analogue of methane. **2** any of a class of saturated silicon hydrides. Such compounds are silicon-containing analogues of alkanes or cycloalkanes; linear or branched silanes are of general formula Si_nH_{2n+2}, and cyclic silanes, termed cyclosilanes, are of general formula $[SiH_2]_n$ ($n > 2$). The value of n, when >1, may be indicated by a specific or general numerical prefix; e.g. disilane, cyclohexasilane, oligosilane, polysilane. Silane and disilane are gases with a repulsive odour; higher silanes are liquids or solids. Silanes are spontaneously flammable in oxygen or air. **3** *a term often loosely applied to* any hydrocarbyl or other derivative of a silane.

silanization treatment of a hydrophilic surface with a reactive **silane** (def. 3) such as dimethyldichlorosilane, trimethylchlorosilane, octyltrichlorosilane, or an octadecyltrialkoxysilane in order to render it more hydrophobic. Such a treatment is useful in particular for converting hydrophilic **silanol** (def. 4) groups on the surfaces of glassware or dried silica-gel particles into lipophilic alkylsiloxane moieties. When applied to glass, it reduces adsorption of polar compounds and minimizes the activation of lymphocytes, platelets, or other cells that can occur when untreated glass vessels are used; other benefits include promotion of drainage of aqueous liquids and minimization of electrical leakage (*see also* **siliconize**). Silanization has been applied to particles of dried silica gel for use in reversed-phase adsorption chromatography (*see also* **end capping**) and to diatomaceous earth used as the support for the stationary phase in reversed-phase liquid–liquid partition chromatography or in some variants of gas–liquid (partition) chromatography. *Compare* **silylation**.—**silanize** *vb.*; **silanized** *adj.*

silanol **1** silyl hydroxide; H_3SiOH; the silicon-containing analogue of methanol. **2** any monohydroxy derivative of a **silane** (def. 2); such compounds are silicon-containing analogues of alkanols and are of general formula $Si_nH_{2n+1}OH$. **3** *a commonly used term for* any *Si*-hydrocarbyl derivative of silanol, silanediol, or silanetriol; such derivatives are respectively of general formula R_3SiOH, $R_2Si(OH)_2$, or $RSi(OH)_3$. **4** the trivalent group ≥Si–OH occurring in hydrated silica (so-called silicic acid). Such groups occur also on the surfaces of dried silica-gel particles and of silica-based glasses under normal conditions (i.e. in equilibrium with undried air).

sildenafil *see* **Viagra**.

silent mutation *or* **synonymous mutation** *or* **same-sense mutation** a mutation in a codon of a DNA sequence that does not cause an amino-acid change in the translation product. The term 'silent' is also applied to a protein gene product arising from such a mutation, e.g. **silent hemoglobin**. *Other names*: silent site mutation; silent nucleotide change.

silica silicon(IV) oxide; silicon dioxide; SiO_2; a colourless or white solid used as the basis of many chromatographic procedures; silicic acid contains **silanol** (def. 4) groups to some of which water is bound. For chromatographic use, it is heated to 100 °C to drive out this water. Heating above 170 °C causes formation of oxide linkages (Si–O–Si), and when heated to very high temperatures (800–1000 °C) it forms glass. Silicic acid is prepared for different uses in a variety of particle sizes. For chromatography, these range from 10 to 500 μm, the larger sizes being used for column chromatography at normal pressures, the smaller sizes for thin layer chromatography and high-pressure liquid chromatography. Silicic acid precipitated as granules, about 3 mm diameter, is known as **silica gel**; in its dry state it takes up water and can be used as a drying agent, which can be re-used after heating to drive out water. A powder of very fine silica particles, 0.007–0.014 μm, known as **fumed silica**, has thixotropic properties and was formerly employed to create a gel in organic solvents, e.g. in scintillation cocktails to maintain hydrophilic materials in suspension during counting (this use is now superseded by cocktails that themselves form a gel with water). Silica is found in certain algae, notably in the hard shell, or test, of diatoms; it also serves to reinforce the stems of the primitive vascular plants known as horsetails.

siliceous *or* **silicious** of, pertaining to, or containing **silica**.

silicone *the common name* for any oligomeric or polymeric **siloxane** containing the repeating structural unit $–O–SiR_2–$, where R is a hydrocarbyl (e.g. methyl or phenyl) group. The molecules of an individual silicone are usually linear, but sometimes branched, crosslinked, or cyclic. Silicones are odourless and generally colourless, and are characterized by high hydrophobicity and by remarkably high chemical and thermal stability. Depending on their molecular size and configuration and on the nature of their R groups, silicones may be oils, greases, gums, elastomers, or resins. By virtue of their unusual and varied properties they have acquired a correspondingly wide range of clinical, electrical, engineering, industrial, and laboratory applications. In commercial usage, the term may be extended to include organosilicon compounds used for **silanization** and **silylation**.

siliconize to render (filter-paper, glassware, textiles, etc.) water-repellent by application of a coating of an appropriate silicone. *See also* **silanization**.—**siliconized** *adj.*; **siliconizing** *n.*

siloxane any saturated silicon-oxygen hydride with unbranched or branched chains of alternating silicon and oxygen atoms in the molecule. Unbranched siloxanes are of general formula $H_3Si–[O–SiH_2]_n–SiH_3$; each is named after its respective parent **silane** (def. 2), e.g. disiloxane ($n = 0$), tetrasiloxane ($n = 2$). By extension, hydrocarbyl derivatives are commonly included. *See also* **silicone**.

silyl **1** *strictly*, $H_3Si–$, the group derived from **silane** (def. 1) by loss of a hydrogen atom. **2** *a commonly used term for* any hydrocarbyl derivative, $R_3Si–$, of the **silyl** (def. 1) group.

silylation the process of converting organic compounds in general into their **silyl** (def. 2) derivatives by attachment of trimethylsilyl (or similar organosilicon) groups, or an instance of this process applied to a particular compound or mixture of compounds. Reagents frequently used for the purpose are trimethylchlorosilane and 1-(trimethylsilyl)imidazole, although a number of others have particular applications. The classes of reactive compounds include those possessing amino, carboxyl, hydroxyl, or thiol groups, for which silylation is a means of selective protection in the course of synthetic work (*see* **protecting group**). Silylation is widely used also for conversion of mixtures of related compounds of such classes into derivatives capable of separation and analysis by gas chromatography/mass spectrometry. *Compare* **silanization**.—**silylate** *vb.*; **silylator** *n.*; **silylated**, **silylating**, *adj.*

simian characteristic of, resembling, or belonging to the apes.

simian immunodeficiency virus *abbr.*: SIV; a retrovirus, one of the lentiviruses, common in the sooty mangabey (a type of monkey) and many African green monkeys. SIV_{SM}, a virus of the sooty mangabey, is closely related to – and probably gave rise to – HIV-2 (*see* **HIV**). HIV-1 is closely related to SIV from chimpanzees. Infection of sooty mangabeys and African green monkeys does not cause disease, but SIV infection has been found in macaques in captivity and is pathogenic.

simian virus 40 *abbr.*: SV40; an icosahedral virus containing circular duplex DNA of about 5.2 kb associated with four histones (H4, H2A, H2B, H3) in a minichromosome. It infects monkeys and apes and is capable of inducing tumours in other species or their cells, its DNA being integrated into the host genome. It can enter two types of life cycle: in permissive cells (usually monkey permanent cell lines) replication occurs in normal infection; in nonpermissive cells there is no lytic infection, but growth transformation can occur. The virus is useful as an **expression vector** in recombinant DNA technology, having good promoter properties: it can be used either as a virion

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or as a construct maintained transiently in host cells at high copy number in unintegrated plasmid-like DNA molecules. *See also* **small T-antigen**.

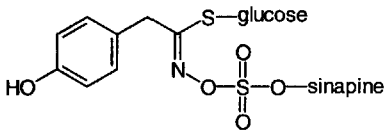
simple diffusion *or* **passive diffusion** a type of **diffusion** (def. 2) across a membrane in the absence of any specific transporting agent or carrier. *Compare* **facilitated diffusion**, **active transport**.

simple radial immunodiffusion *see* **single radial immunodiffusion**.

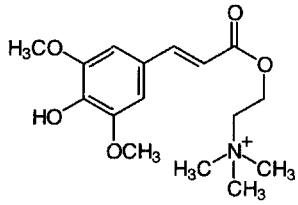
SIMS *abbr. for* secondary ion mass spectrometer.

sin *abbr. for* sine.

sinalbin a glucoside found in white or yellow mustard. *See also* **sinapine**.



sinapine 2[[3-(4-hydroxy-3,5-dimethoxyphenyl)-1-oxo-2-propenyl]oxy]-*N*,*N*,*N*-trimethylethanaminium; a component of **sinalbin**; it is also found in black mustard and other seeds.



sinaptobrevin *a variant spelling of* **synaptobrevin**.

sine *abbr.*: sin; a trigonometric function, being the ratio of the side of a right-angled triangle opposite a given angle to the hypotenuse; the sine of an obtuse angle is numerically equal to that of its supplement.

SINE *abbr. for* short interspersed element; a highly repeated sequence of DNA occurring interspersed in a mammalian genome; it is similar to a **LINE** but is shorter – typically less than 500 bp long – and is generated by **RNA polymerase** III. A family of closely related SINEs has of the order of 10^5 members, consisting of DNA segments that are similar if not identical in length and sequence. The function of SINEs is unknown. They appear to be processed **pseudogenes** derived from genes that encode small cytoplasmic RNAs including tRNAs. Thus the sequences of SINES are often homologous to the sequences of such RNAs.

Singer–Nicholson model *an alternative name for* **fluid-mosaic model**.

single-cell protein *abbr.*: SCP; a protein-rich material produced by the culture of bacteria, yeasts, other fungi, or algae and extracted for use as a protein supplement in animal or human foods.

single-copy plasmid a plasmid that replicates at the same pace as the bacterial chromosome, and thus maintains equality in numbers with the chromosome.

single nucleotide polymorphism *abbr.*: SNP; the occurrence of single-base variations in the genetic code that occur about once every 1000 bases along the human genome.

single radial immunodiffusion *or* **Mancini method** an **immunodiffusion** technique in which holes (wells) are cut in a sheet of antibody-containing agar in a glass dish or on a slide. The wells are filled with antigen solution, which is then left to diffuse radially outwards; in doing so, it reacts with antibody to form a ring of precipitate. The diameter of the circle of precipitate is proportional to the concentration of antigen.

single-spanning describing an integral membrane protein anchored in the membrane by means of a single hydrophobic sequence embedded in the membrane lipid bilayer.

single-strand binding protein *abbr.*: SSB protein; any of a group of proteins found in bacteria and mitochondria that have a greater affinity for **single-stranded DNA** than for double-stranded species. They are essential for replication, recombination, and repair. They bind tightly and cooperatively and do not catalyse associated activities such as the DNA-dependent ATPase activities of **helicases** and **topoisomerases**. They have been called 'unwinding', 'melting', and 'helix-destabilizing' proteins, but each of these names is somewhat misleading since these proteins have multiple functions. Example from *Escherichia coli*: database code SSB_ECOLI, 177 amino acids (18.82 kDa).

single-strand conformation polymorphism analysis *abbr.*: SSCP analysis; a method for comparing mutations by the rate at which DNA migrates on denaturing gels, under conditions in which the conformation adopted by the DNA is critical. The technique involves amplification of a DNA sequence of interest using the **polymerase chain reaction** (PCR); the rate of migration of this DNA is then compared with that of a known mutation on gels of differing composition, such that DNA conformation (and thus rate of migration) will depend on the gel conditions (e.g. varying glycerol concentration, ionic strength). If the DNA of unknown composition migrates the same as the known DNA under all conditions, it is an indication that a mutation of a similar character to the known mutation may have occurred.

single-stranded DNA *abbr.*: ssDNA; a form of **DNA** consisting of a single chain of deoxyribonucleotides instead of the normal two chains. Single-stranded DNA occurs naturally in certain circumstances: (1) transiently, during replication (*see* **replicate**), when the duplex helical molecule of double-stranded DNA is unwound in the replication fork, initiated by **helicase**; (2) during replication of circular DNA, when in some circumstances only one strand is replicated, yielding a single-stranded product; as replication proceeds, the synthesized DNA unwinds as a single-stranded 'tail'. Replication may proceed around the unbroken circular DNA strand for more than one cycle, giving rise to the term **rolling circle**; (3) in certain filamentous **coliphages**, such as M13, f1, and fd, which contain a single-stranded circular DNA molecule.

singlet oxygen a dioxygen molecule in which two 2p electrons have similar spin. It is more highly reactive than the form in which these electrons are of opposite spin. Singlet oxygen is produced in chloroplasts that, due to mutation, lack carotenoids; excited triplet chlorophyll reacts with oxygen to yield singlet oxygen, which is normally quenched by carotenoids. In the absence of carotenoids, lethal photodynamic damage occurs.

single-turnover kinetics the study of the kinetics of an enzyme-catalysed reaction in conditions under which formation of the enzyme–substrate complex can be measured. Such conditions are required for the detection and analysis of transient enzyme–substrate and enzyme–intermediate forms in the investigation of the pre-steady state (*see* **pre-steady state kinetics**), and contrast with measurement of the multiple recycling of the enzyme in the steady state. Although the enzyme reaction is proceeding normally, only the first part of the reaction is studied, leading to the expression 'single-turnover conditions'. In this kind of study, a substrate is chosen such that the enzyme–substrate complex can be distinguished from substrate alone, e.g. in having a different absorption spectrum. The rate of formation of the complex can then be determined, often by stopped-flow methods.

singly labelled describing a **specifically labelled** compound containing only one isotopically modified atom in a uniquely specified position, e.g CH_3–$CH[^2H]$–OH.

sinigrin 1-thio-*β*-D-glucopyranose 1-[*N*-(sulfo-oxy)-3-butenimidate] monopotassium salt; a *β*-D-thioglucoside occurring in

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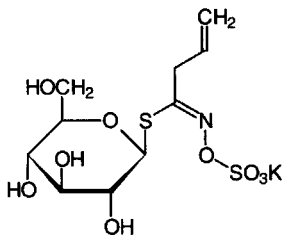
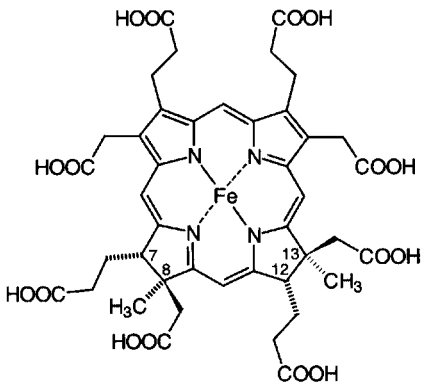
mustard seeds and horseradish roots; it is used as a substrate for thioglucosidase.



sinister *Latin* left; used to describe the left, or counterclockwise, configuration of one of the two faces of a compound containing a trigonal carbon atom. It is designated by the prefix *Si-*. *Compare* ***rectus***. *See also* ***Re/Si* convention**.

sintered glass *or* **frit** small particles of glass that have been heated so that they just fuse but without extensive melting. The resultant material is porous, and is often used in glass filtration apparatus or as a support to retain packing materials in chromatographic columns.

siroheme *or (esp. Brit.)* **sirohaem** a heme molecule discovered in bacterial sulfite reductase, EC 1.8.99.1. It is a tetrahydroporphyrin, having adjacent, reduced pyrrole rings. It is also a component of nitrite reductase (EC 1.6.6.4) from *Nitrobacter*.



siroheme synthase *or (esp. Brit.)* **sirohaem synthase** a multifunctional bacterial enzyme that contains **uroporphyrin-III C-methyltransferase**, **ferrochelatase** and precorrin-2 oxidase. The latter activity results in the conversion of precorrin-2 into **siroheme** by oxidation and Fe^{2+} chelation. Example from *Escherichia coli*: database code CYSG_ECOLI, 457 amino acids (49.90 kDa).

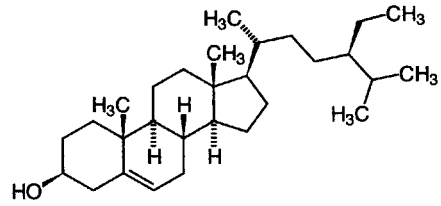
sirup *a variant spelling (esp. US) of* **syrup**.

sis an oncogene (v-*sis*) from simian osteosarcoma virus that is also expressed in human disease. The related protooncogene, c-*sis*, encodes the B chain of **platelet-derived growth factor** (PDGF), and v-*sis* encodes a protein almost identical to the B chain, differing only in the amino acids at its N and C termini. Cells are transformed by v-*sis* and produce the PDGF-related molecules, which stimulate the PDGF receptor in an autocrine fashion. Example, PDGF-related transforming protein $p28^{sis}$ of simian sarcoma virus: database code TSIS_SMSAV, 226 amino acids (25.42 kDa).

site-directed mutagenesis *or* **site-specific mutagenesis** the use of cDNA technology to generate a **point mutation** at a predetermined position in a genome. It may be achieved by stepwise synthesis of a strand of genomic nucleic acid with substitution of a mutagenic analogue of the base naturally present (e.g. guanine for adenine) at a specific position in the nucleotide sequence. After purification this is replicated *in vitro* to allow the generation of base substitutions at the corresponding site in the complementary strand.

site-specific DNA methyltransferase *see* **DNA methylase**.

sitosterol 22,23-dihydrostigmasterol; a widely distributed plant sterol related to **stigmasterol**.



β-sitosterol

SI units *see* **SI**.

SIV *abbr. for* simian immunodeficiency virus.

sizing column a **gel-filtration** column that is used to provide information about the M_r (size) of proteins.

sizing gel a **gel-filtration** medium, especially one used in a sizing column.

sizukacillin *see* **peptaibophol**.

S2 kallikrein *see* **tonin**.

SKALP *abbr. for* skin-derived antileukoproteinase; *other name* elafin; an inhibitor of serine proteinases; it probably inhibits elastase-mediated tissue proteolysis. Example, human protein sequence (precursor): database code ELAF_HUMAN, 117 amino acids (12.26 kDa).

skatole 3-methylindole; a bacterial metabolic product of indoleacetic acid that contributes to the odour of feces.

skeletal growth factor a protein that stimulates bone growth. Skeletal growth factor from human bone (hSGF) stimulates growth in human bone cells and embryonic chick bones in culture. The activity comprises **insulin-like growth factors** (IGFs) in association with IGF-binding proteins (IGFBPs). Example, precursor of human IGFBP-5: database code IBP5_HUMAN, 272 amino acids (30.53 kDa).

skeletin *(formerly) an alternative name for* **desmin**.

skeleton **1** *(in zoology)* any structure that provides support and protection for the soft tissues and organs of the body. An **exoskeleton**, such as the cuticle in arthropods, lies external to the body tissues, while an **endoskeleton**, such as the bony or cartilaginous skeleton of vertebrates, lies within the body. **2** *(in chemistry)* the carbon chain of a molecule, including any noncarbon elements that necessarily link carbon moieties of the chain. —**skeletal** *adj.*

skew **1** asymmetric, biased, distorted. **2** oblique, slanting. **3** (of a statistical distribution) not symmetrical about the mean. **4** to become or make skew; to distort. *See also* **skew conformation**. —**skewness** *n.*

skew conformation **1** any conformation of a six-membered ring form of a monosaccharide or monosaccharide derivative when three adjacent ring atoms and the remaining nonadjacent ring atom are coplanar. Such compounds may be designated by the conformational descriptor *-S* added to the name. The reference plane is so chosen that the lowest-numbered carbon atom in the ring, or failing that the atom numbered next above it, is exoplanar. Skew conformation is the median conformation through which one **boat conformation** passes during conversion to another boat conformation in the cycle of flexible forms; it is similar to **twist conformation** (def. 1). *See also* **conformation**. **2** *a less common alternative term for* synclinal conformation; *see* **conformation**.

SKI a gene encoding a protein of unknown function but related to v-*ski*, the oncogene of Sloan-Kettering viruses; it has no marked homology with other oncogenes.

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slab gel a gel, usually polyacrylamide or starch, that is formed as a sheet rather than a rod.

slaty a coat colour mutation in mice allelic for the *tyrp-2* gene. The mice have a defect in melanin formation that causes dark-grey (slate-coloured) melanin to be formed. The enzyme affected is **dopachrome Δ-isomerase**.

sleep peptide any peptide that brings about sleep when infused into the cerebrospinal fluid (CSF) of animals. Delta-sleep-inducing peptide, isolated from CSF, has the structure Trp-Ala-Gly-Gly-Asp-Ala-Ser-Gly-Glu. A large number of endogenous substances isolated from the brain can likewise induce sleep, but it is not known if this is their physiological function.

sliding filament model a model of muscle contraction that envisages contraction occurring as a result of **thin filaments** sliding past **thick filaments**. The mechanism of activation involves enhanced binding of Ca^{2+} by troponin C (*see* **troponin**), one of the three troponin peptide components of the thin filament. In the resting state, troponins I and T inhibit the actin–tropomyosin complex of the thin filament from binding to myosin; increase in Ca^{2+} concentration causes troponin C (each molecule of which binds up to four Ca^{2+} ions) to release this inhibition, allowing the myosin headgroups to bind actin. Then, in the presence of ATP, the thin filaments slide over the thick filament myosin molecules to cause contraction. The myosin heads contain an active ATPase that hydrolyses the ATP; the latter must be continuously resynthesized for contraction to continue.

sliding (of repressor) the mode of action of ***lac* repressor** in *Escherichia coli*. It first binds at a non-operator site, then slides along the DNA until it finds the target site, i.e. the **operator**.

slime mould *or (US)* **slime mold** any of a group of organisms that exhibit features of both fungi and protozoa. Characteristically they exist as slimy masses on decaying wood or in damp soil, and have the ability to switch from an amoeboid single-celled phase, called a **myxamoeba**, to an aggregated or multicellular phase from which fruiting bodies may arise. In the so-called **true slime moulds**, the myxamoebae form an acellular mass called a plasmodium, whereas in the **cellular slime moulds** the myxamoebae aggregate to form a multicellular pseudoplasmodium, or 'slug'. A well-known example of a cellular slime mould is *Dictyostelium discoideum*; when the food supply is exhausted, its myxamoebae aggregate to form a small (1–2 mm) slug, containing up to 10^5 cells, which migrates to seek an area of food abundance. When nutritional conditions are favourable the slug undergoes differentiation to form fruiting bodies, from which spores are released. Germination of a spore leads to the formation of a myxamoeba. *D. discoideum* has a relatively small genome (about 10 times larger than that of a bacterium) and is popular with geneticists, providing insights into the nature of the inducible behaviour leading to aggregation, and the rapid cell division and differentiation that precede the formation of a fruiting body.

slip a term used in regard to situations in which the mitochondrial enzyme, **cytochrome *c* oxidase**, may carry out its redox reaction without pumping protons into the intermembrane space.

slope $\delta y/\delta x$, where results are expressed graphically as a continuous line, the ordinate (vertical axis) representing y, the abscissa (horizontal axis) representing x.

slow-cycling rhodopsin a **retinal**-containing energy-transducing pigment present in small amounts in some of the strains of *Halobacterium halobium* in which purple membranes occur. It is distinct from **bacteriorhodopsin** and **halorhodopsin** and is believed to play a role in the characteristic variation in the phototactic response of such organisms at different wavelengths. Illumination with yellow light or with blue or near-ultraviolet light results respectively in accumulation of forms with absorption maxima at 375 nm and 590 nm.

slow reacting substance (of anaphylaxis) *or* **slow reacting substance A** *abbr.*: SRS *or* SRS-A; one of a number of substances that mediate anaphylaxis; it was identified as a polar, lipid-like compound not normally present in mammalian tissues but synthesized in them as a consequence of the combination of antibody with antigen. It increases vascular permeability and induces contraction of some types of smooth muscle, especially bronchial muscle. It is slow in action relative to histamine – hence its name – and is not antagonized by antihistamines. **Leukotrienes C_4**, **D_4**, and **E_4** are now known to be the active components.

slurry a fluid suspension of particles having the consistency of cream.

Sm *symbol for* samarium.

small cytoplasmic ribonucleoprotein *abbr.*: scRNP (hence often colloquially termed 'scyrp'); any of various particulate complexes of proteins with molecules of **small cytoplasmic RNA**, found in the cytoplasm. Their function is unknown.

small cytoplasmic RNA *abbr.*: scRNA; any of various low-molecular mass (100–300 nucleotides) RNA molecules found in the cytoplasm as components of **small cytoplasmic ribonucleoprotein**.

small intensely fluorescent cell *abbr.*: SIF cell; a cell found in autonomic ganglia and containing dopamine. The name derives from the appearance of such cells after formaldehyde condensation in fluorescence microscopy.

small nuclear ribonucleoprotein *abbr.*: snRNP (hence often colloquially termed 'snurp'); any of various particulate complexes of proteins with molecules of **small nuclear RNA** (snRNA), found in the eukaryotic nucleus; the particles are ≈250 kDa. They are named according to the snRNAs they contain: the U4/U6 snRNP, e.g., contains U4 and U6 snRNA. They are involved in RNA splicing (*see* **spliceosome**). Patients with systemic lupus erythematosus make antibodies directed against one or more snRNPs.

small nuclear RNA *abbr.*: snRNA; any of various low-molecular-mass (100–300 nucleotides) RNA molecules, designated U1, U2, ... U12 RNA, found in the eukaryotic nucleus as components of **small nuclear ribonucleoprotein**. *See also* **spliceosome**.

small nucleolar ribonucleoprotein *abbr.*: snoRNP (hence often colloquially termed 'snorp'); any of various particulate complexes of proteins with molecules of **small nucleolar RNA**, found in the eukaryotic nucleolus. They are possibly the same as **processosomes**.

small nucleolar RNA *abbr.*: snoRNA; any of a class of small RNAs that are associated with the eukaryotic nucleus as a component of **small nucleolar ribonucleoproteins** and participate in the processing of ribosomal RNA. They contain a long stretch of sequence complementarity to conserved sequences in mature mRNA. Six have been identified in metazoan cells (87–280 bases) and 12 in yeast (125–605 bases). They exist as ribonucleoprotein (RNP) particles, which appear to assemble with a large multi-RNA RNP complex.

small T-antigen *see* **T-antigen** (def. 1).

S_1 mapping *or* **S_1 nuclease mapping** a commonly used technique depending on the property of **S_1 nuclease** to remove single-stranded DNA or RNA from double-stranded hybrids of DNA and RNA. It may be used to detect the coding region of genomic DNA that contains **introns** by a procedure in which either cDNA for a particular mRNA or the mRNA itself is hybridized to the genomic DNA, and the single-stranded DNA removed by the S_1 nuclease leaving the hybridized coding DNA (the exons). The enzyme can also be used in a similar way to identify the 5′ end of a mRNA.

smectic (of a substance) being or having a **mesomorphic** state in which the molecules are arranged in parallel layers. The molecules in any layer can move in the plane of that layer but not into adjacent layers. *Compare* **nematic**. *See also* **liquid crystal**.

smectic mesophase *see* **liposome**, **liquid crystal**.

Smith **1 Hamilton Othanel** (1931–), US molecular biologist; Nobel Laureate in Physiology or Medicine (1978) jointly with W. Arber and D. Nathans 'for the discovery of restriction enzymes and their application to problems of molecular genet-

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ics'. **2 Michael** (1932–), British-born Canadian biochemist; Nobel Laureate in Chemistry (1993) 'for his fundamental contributions to the establishment of oligonucleotide-based, site-directed mutagenesis and its development for protein studies' [prize (awarded 'for *contributions to the developments of* methods within DNA-based chemistry') shared with K. B. Mullis].

smooth describing a bacterial strain having shiny (smooth) colonies. *See* **smooth–rough variation**.

smooth endoplasmic reticulum *abbr.*: SER; *see* **endoplasmic reticulum**.

smooth muscle *or* **involuntary muscle** muscle that lacks striations, hence giving a 'smooth' appearance under the microscope; it produces slower, longer lasting contractions than **striated muscle** and is responsible for the contractile function of visceral organs such as stomach, bladder, intestine, and uterus, and the walls of arteries. The cells are mononucleate, and contain both **thick filaments** and **thin filaments** although these are not arranged in the pattern that leads to striations in skeletal muscle and cardiac muscle. The thin filaments are composed mainly of actin, polymerized into a double-helical strand, and associated with tropomyosin arranged along the length of the actin filament. The thick filaments are composed of aggregated myosin molecules. The thick and thin filaments comprise the contractile elements and are thought to function in an analogous manner to their striated muscle counterparts (*see* **sliding filament model**). Muscle contraction is regulated by the sarcoplasmic (cytosolic) free Ca^{2+} concentration, which increases from resting levels of 120–270 nM to 500–700 nM in response to stimuli such as membrane depolarization, or the action of α-adrenergic or muscarinic agonists. Ca^{2+} then binds to calmodulin, which activates **myosin-light-chain kinase**, which phosphorylates myosin at Ser^{19} of each of the two 20 kDa light chains. This causes cycling of myosin cross-bridges along actin filaments and the development of force. **Calponin**, **caldesmon**, and **protein kinase C** are also thought to play a role in fine-tuning the contractile state.

smooth–rough variation *or* **S→R variation** any of a number of types of cell-surface compositional variation that occur in bacteria, usually giving rise to changes in the appearance of colonies from that of the original strain. In the Enterobacteriaceae the colonies are typically shiny (smooth) and change to matt (rough), an S→R variation that may be accompanied by loss of surface antigens, reduction or loss or virulence, and changes in susceptibility to certain bacteriophages.

sn- *prefix (in chemical nomenclature)* signifying stereospecifically numbered; it is used in designating the configuration of derivatives of certain classes of prochiral compounds (especially glycerol and its derivatives) to ensure differentiation from conventional numbering. Thus sn-1 denotes C-1 of the glycerol moiety of a phospholipid under the **stereospecific numbering** system. C-2 and C-3 are similarly denoted *sn*-2 and *sn*-3 under the same system.

Sn *symbol for* tin.

SNAP *abbr. for* **1** *S*-nitroso-*N*-acetylpenicillamine. **2** synaptosome-associated protein; a number of these exist. The nomenclature has become somewhat confusing, since SNAPs exist with different but closely related roles. Thus SNAP-25 functions as a SNAP receptor, or **SNARE**, while other SNAP proteins such as α-SNAP (*see* def. 3) function to bind NSF proteins (*see* ***N*-ethylmaleimide**) to SNAREs such as SNAP-25. Example, SNAP-25 from chicken and mouse neurons: database code SN25_MOUSE, 206 amino acids (23.29 kDa). **3** soluble NSF attachment proteins, such as α-SNAP, β-SNAP, etc. These are cytoplasmic proteins that mediate binding of ***N*-ethylmaleimide-sensitive fusion protein** to membranes. *See also* **SNARE, SNARE hypothesis**.

SNARE *abbr. for* SNAP receptor; **syntaxin**, **synaptobrevin**, and SNAP-25 (*see* **SNAP** (def. 2)) act as SNAREs; they bind in an ATP-dependent manner to NSF–SNAP complexes (SNAP in this case being the NSF attachment protein (*see* ***N*-ethylmaleimide**)). Syntaxin, synaptobrevin, and SNAP-25 form a complex that is much more effective than the single proteins acting alone, leading to the concept of a core complex that bridges the synaptic vesicle and plasma membranes, and which *may function in the docking and fusion process*. *See also* **SNARE hypothesis**.

SNARE hypothesis a suggested model of vesicular fusion, in which two types of **SNARE** are involved; v-SNAREs are found on vesicles and t-SNAREs are found on the target membranes, each transport vesicle having its own v-SNARE which recognizes a cognate t-SNARE on a target membrane and mediates docking; fusion is then mediated by *N*-ethylmaleimide-sensitive fusion protein and an attachment protein (**SNAP** (def. 3)).

Snell, George Davis (1903–96), US geneticist; Nobel Laureate in Physiology or Medicine (1980) (jointly with B. Benacerraf and Jean Dausset 'for their discoveries concerning genetically determined structures on the cell surface that regulate immunological reactions').

Snell's law *see* **refraction**.

Sno *symbol for* a residue of the ribonucleoside thioinosine; mercaptopurine ribonucleoside; alternative to sI.

snoRNA *abbr. for* small nucleolar RNA.

snoRNP *abbr. for* small nucleolar ribonucleoprotein.

snorp *colloquialism* for snoRNP, i.e. **small nucleolar ribonucleoprotein**.

snRNA *abbr. for* small nuclear RNA.

snRNP *abbr. for* small nuclear ribonucleoprotein.

S_1 nuclease EC 3.1.30.1; *recommended name*: *Aspergillus* nuclease S_1; a single-strand endonuclease, purified from *Aspergillus oryzae*, that degrades single-stranded RNA or DNA to 5′ mononucleotides; it has no apparent base specificity. It is useful for the removal of unpaired regions in hybridization technology (*see also* **S_1 mapping**). The enzyme is a monomer, and contains three zinc atoms. Database code NUS1_ASPOR, 267 amino acids (29.02 kDa). Similar enzymes occur in *Penicillium* spp. and barley.

snurp *colloquialism for* snRNP, i.e. **small nuclear ribonucleoprotein**.

snurposome any of at least three (A, B, and C) morphologically and biochemically distinct granules in the amphibian oocyte nucleus that contain one or more types of small nuclear ribonucleoproteins (snRNP).

soap any salt formed between a hydroxide of a metal (usually an alkali or alkaline earth) and a higher fatty acid; such compounds are useful as **detergents** (def. 2). The meaning is sometimes extended to include the salt of any ionized lipid **amphipath**, e.g. of a long-chain amine or sulfate or of a sterol carboxylate. The common soaps of commerce were traditionally the mixed sodium salts (giving **hard soaps**) or the mixed potassium salts (giving **soft soaps**) of oleic, palmitic, and stearic acids, prepared by **saponification** of animal or vegetable fats or oils with sodium or potassium hydroxide respectively. Modern soap compositions are more complex, with solid or liquid soaps containing various additional detergents.

soapstone *see* **talc**.

SOD *abbr. for* superoxide dismutase.

soda any of various compounds of sodium, especially sodium hydroxide (NaOH; **caustic soda**), sodium hydrogencarbonate (sodium bicarbonate, $NaHCO_3$; **baking soda**), or sodium carbonate decahydrate ($Na_2CO_3{\cdot}10H_2O$; **washing soda**). The term may also indicate sodium monoxide (Na_2O).

soda glass common glass, made from a mixture of silica, sodium oxide (soda), and lime, in approximate proportions SiO_2 70%, Na_2O 15%, CaO 10%. Its low melting point led to the production of more heat-resisting glasses, e.g. Pyrex. *See also* **borosilicate (glass)**.

Soddy, Frederick (1877–1956), British inorganic and physical chemist; Nobel Laureate in Chemistry (1921) 'for his contributions to our knowledge of the chemistry of radioactive substances, and his investigations into the origin and nature of isotopes'.

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sodium *symbol*: Na; a soft, silvery-white, highly reactive alkali metal of group 1 of the (IUPAC) **periodic table**; atomic number 11; relative atomic mass 22.997. Sodium is widely distributed and is one of the most abundant elements of the Earth's crust; it exists in great quantity as sodium chloride (salt), especially in sea water. Apart from the nonradioactive, and most abundant, isotope, sodium-23, there are two radioactive isotopes, **sodium-22** and **sodium-24**. In biochemistry, sodium (Na^+) is the principal extracellular cation, and the one that largely determines the extracellular fluid volume. In humans the normal range for plasma sodium is 135–145 mmol L^{-1}. Sodium ions are actively pumped out of cells by **sodium/potassium ATPase**. Their concentration in the blood is regulated by the mineralocorticoid hormone **aldosterone**, which increases sodium reabsorption in the kidney distal tubule. In scientific and medical literature sodium was formerly given the Latin name 'natrium', hence the symbol Na and the term **natriuretic**.

sodium-22 a radioactive nuclide of sodium, $^{22}_{11}Na$. It emits a β^+ particle (1.83 MeV) and gamma radiation (1.275 MeV). Its half-life is 2.605 years.

sodium-24 a radioactive nuclide of sodium, $^{24}_{11}Na$. It emits an electron (β^- particle, 1.39 MeV) and gamma radiation (2.75 MeV). Its half-life is 15.02 h.

sodium–alanine symporter *see* **sodium/neutral amino acid cotransporter**.

sodium–calcium ion exchanger a plasma membrane protein **antiporter** of muscle and nerve cells that promotes the exchange diffusion of sodium and calcium ions. Influx of Na^+ to the cytosol drives the efflux of Ca^{2+} from the cell. The affinity for Ca^{2+} is low, so that it only functions at high intracellular Ca^{2+} concentrations, transporting Ca^{2+}, e.g., during excitation–contraction coupling. Example from human cardiac sarcolemma, type III membrane glycoprotein (precursor): database code NACA_HUMAN, 973 amino acids (108.42 kDa).

sodium channel any of several types of structure that permit controlled (gated) passage of sodium ions through membranes. Two important types of gated sodium-ion channels are the voltage-gated channel and the transmitter-gated channel. Voltage-gated channels are involved in conduction and transmission of nerve impulses, whereas transmitter-gated channels respond only to neurotransmitters; a well-studied example of the latter type of channel is the **acetylcholine receptor**. Voltage-gated sodium-ion channels consist of integral proteins in the plasma membranes of excitable cells. The proteins sense the membrane electric field, opening channels to permit an inward flux of sodium ions, thereby causing the membrane depolarization that is essential for the propagation of the **action potential**. Primary sequence data for the *Electrophorus* electroplax protein indicate that this channel consists of a single polypeptide chain of about 2000 amino-acid residues and contains four homologous repeats (domains I, II, III, and IV), each of which has six putative transmembrane segments (designated S1 to S6) with extensive nonmembrane cytosolic and extracellular loops. This sequence shares significant homology to other ion channels, particularly the α1 subunit of the Ca^{2+} channel, segment S4 showing strong structural similarity to sequences in the Ca^{2+} and K^+ channels. The cytoplasmic loop between repeats III and IV has been implicated in the rate of inactivation of the channel. As normally expressed the protein bears about 500 sugar residues (mostly *N*-acetylglucosamine and sialic acid) and 50 fatty-acyl chains (palmitoyl and stearoyl). Structural data are also available for enzymes of *Drosophila* and mammalian skeletal muscle and brain. The mammalian channels are heterooligomeric, consisting of a large α subunit similar to the *Electrophorus* protein, and several other smaller peptides; most of the functional properties reside in the α subunit. Example from rat brain (large subunit): database code CIN1_RAT, 2009 amino acids (228.51 kDa); seven motifs. The α subunit is the target for polypeptide neurotoxins, e.g. from scorpions; other sodium-channel blockers include **saxitoxin**, **tetrodotoxin**, and **veratridine**.

sodium dodecyl sulfate *or (esp. Brit.)* **sodium dodecyl sulphate** *abbr.*: SDS; sodium lauryl sulfate; $CH_3(CH_2)_{10}CH_2OSO_3{\cdot}Na$; the sodium salt of the 1-dodecanol half-ester of sulfuric acid (1-dodecanol was formerly known as lauryl alcohol). It is an anionic detergent and wetting agent; aggregation number 62 (0–0.1 M Na^+), 101 (>0.1 M Na^+); CMC 7–10 mM (0–0.05 M Na^+), 1–2 mM (0.1–0.2 M Na^+). The amphipathic dodecylsulfate anion is a powerful hydrophobic-bond breaker, hence it is much used in protein chemistry as, e.g., a denaturant, a dissociant of oligomers, and a solubilizer of membrane components. *See also* **SDS–polyacrylamide gel electrophoresis**.

sodium–hydrogen ion exchanger a plasma membrane protein that functions as a Na^+/H^+ **antiporter**. Influx of Na^+ drives the efflux of H^+. It functions to maintain intracellular pH, to which it is sensitive, its activity increasing as pH falls. Example from the gills of the crab, *Carcinus maenas*: database code CMU09274, 672 amino acids (75.89 kDa).

sodium-ion channel *see* **sodium channel**.

sodium/neurotransmitter transporter any of a family of integral membrane glycoproteins, having eight motifs and 12 putative transmembrane helices, that are involved in sodium-dependent transport of neurotransmitters. Examples (precursors) include sodium-dependent choline transporter from rat: database code NTCH_RAT, 635 amino acids (70.55 kDa); sodium- and chloride-dependent GABA transporter 1 from human: database code NTG1_HUMAN, 599 amino acids (66.94 kDa). This latter protein is the target for cocaine and other psychomotor stimulants.

sodium/neutral amino-acid cotransporter an integral membrane protein responsible for the Na^+-dependent uptake of the neutral amino acids alanine, serine, glycine, cysteine, and proline. Example from pig: database code NAAA_PIG, 660 amino acids (72.66 kDa). Transporters with specificities for different types of amino acid are **system A**, **system L**, and **system N**.

sodium/potassium ATPase EC 3.6.1.37; *recommended name*: Na^+/K^+-exchanging ATPase; *systematic name*: ATP phosphohydrolase (Na^+/K^+-transporting); *other names*: sodium pump; Na^+,K^+-ATPase. An integral membrane protein that catalyses the hydrolysis of ATP to ADP and orthophosphate. Na^+,K^+-ATPases are **integral (cell membrane) proteins**, and pump out approximately 3 Na^+ ions for every 2 K^+ ions that enter, with hydrolysis of 1 ATP. They are tetrameric proteins, consisting of two large α subunits and two smaller β subunits. The α subunits bear the active site and penetrate the membrane, while the β subunits carry oligosaccharide groups and face the cell exterior only. **Ouabain** is a specific inhibitor. Examples from rat; α-1 chain: database code ATN1_RAT, 1023 amino acids (112.92 kDa); β chain: database code ATNB_RAT, 304 amino acids (35.16 kDa); γ chain: database code ATNG_RAT, 58 amino acids (6.49 kDa).

sodium pump any of various **transporters** that transport sodium ions across membranes, especially enzymes of the Na^+,K^+-ATPase type (*see* **sodium/potassium ATPase**). The Na^+/K^+ ratio across the plasma membrane of eukaryotic cells (outside: Na^+ 140 mM, K^+ 10 mM; inside: Na^+ 10 mM, K^+ 100 mM) requires that sodium ions be continually pumped out of the cell in exchange for potassium ions if the gradient is to be maintained; this is an energy-requiring process. *See also* **active transport**.

software *(in computing)* programs used by computer hardware to execute commands keyed or otherwise supplied by the computer operator to bring about the completion of desired tasks. Most software is not permanently resident in the computer but is accessed from disks as instructed by the operator, **operating systems**, or other software.

sol any fluid colloidal system composed of two or more components. The dispersed phase may be either particles of solid or droplets of liquid, and the continous phase either a liquid or a gas (*see* **aerosol**).

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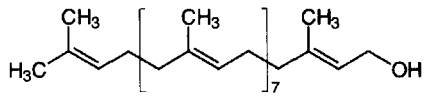
solanesol a 45-carbon polyprenol present in tobacco leaves.



solation the (usually reversible) act or process of forming a **sol** from a **gel**. *Compare* **gelation**. —**solate** *vb.*

solid a physical state of matter in which the constituent atoms, ions, or molecules have no translatory motion though they vibrate about fixed positions. In **crystalline solids** the constituents are arranged in a definite array, whereas in **amorphous solids** they are not. Solids, especially crystalline solids, commonly have characteristic melting temperatures at which they change to **liquids**.

solid-phase peptide synthesis *see* **peptide synthesis**.

solid-phase technique any technique in which reagents are immobilized on a support or in some other way insolubilized. In **radioimmunoassay** the insolubility or binding properties of an antigen–antibody complex are commonly exploited to remove labelled antigen. Enzymes immobilized on columns (**immobilized enzymes**) have many applications. In **peptide synthesis**, the growing peptide chain may be immobilized on a column. So-called solid-phase extraction systems are in effect extractions using batch column chromatography techniques, in which the material to be extracted is bound to a column, then removed by **batch elution**. In peptide **sequencing** a peptide immobilized on a column may be degraded residue by residue, facilitating recovery of the undegraded remaining peptide at each cycle.

solid scintillation fluorography a technique for visualizing radioactive materials in a specimen (e.g. a chromatogram) by covering the specimen with a solid **fluor** and allowing the ejected photons to darken an applied photographic emulsion. *Compare* **fluorography** (def. 2).

solid-state *(in electronics)* describing any system in which current flow takes place entirely through solid materials, such as semiconductors and transistors, rather than through vacuum devices such as thermionic valves.

solubility **1** the attribute of being soluble, of being able to dissolve. **2** the amount of a substance (**solute**) that can dissolve in a given amount of another substance (**solvent**) at a given temperature and pressure.

solubility product *symbol*: K_{sp}; for a solute A_xB_y that ionizes in a stated solvent according to the equilibrium $A_xB_y \rightleftharpoons xA + yB$, at a given temperature and pressure, $K_{sp} = [a_A]^x[a_B]^y$, where $[a_A]$ and $[a_B]$ are the activities of the two ions when the solution is saturated by the solute. In unsaturated solutions the product $[a_A]^x[a_B]^y$ can have any value less than K_{sp}, but if further amounts of either ion are added from whatever source, such that K_{sp} is exceeded, precipitation from solution will occur to the extent that the relationship $[a_A]^x[a_B]^y = K_{sp}$ is restored. In dilute solutions the concentrations C_A and C_B of A and B may be used as a good approximation.

solubilize *or* **solubilise** to bring into solution any material, especially complexes that normally exist in the cell as part of membrane structures. Such materials usually have hydrophobic domains, and solubilization depends on masking these with detergents or similar substances, to bring the material into micellar suspension.

soluble **1** capable of being dissolved in or as if in a fluid. **2** (of, e.g., a problem or mathematical equation) capable of being solved.

soluble collagen *see* **tropocollagen**.

soluble RNA *abbr.*: S-RNA *or* sRNA; *an old term for* **transfer RNA** (a 'soluble' RNA fraction from disrupted liver cells that did not sediment after centrifuging at 100 000 *g* for several hours led to the discovery of transfer RNA).

solute a dissolved substance, particularly a component of a **solution** that is present in a smaller amount than the **solvent**.

solution **1** a homogeneous molecular mixture of two or more substances, usually of dissimilar molecular structures, i.e. of a solid in a liquid. **2** the action or process of solving a problem. **3** the result of solving a problem, equation, etc.

solvation the (loose) combination of solvent with molecules or ions of the solute.

solvation effect the effect of solvent molecules on the behaviour of (especially) macromolecules in solution, especially during centrifugation.

solvent **1** a substance or mixture, usually a liquid, that is able to dissolve other substances to form a solution. Typically it has the same physical state as the solution itself, and is the component of greatest extent in the solution. **2** *(in chromatography)* the liquid used to pass through a chromatography column, paper, or other support to 'develop' the chromatogram.

solvent-perturbation method a technique in which some physical property of a macromolecule is measured in a polar and in a nonpolar solvent. For example, it can be determined whether an amino-acid residue in a protein is internal or external by measuring the absorption spectra of the protein in the two types of solvents. Difference spectroscopy is conveniently applied in such instances.

soma (*pl.* **somata** *or* **somas**) **1** the whole of any plant or animal organism but excluding the germ cells. **2** the body, as opposed to the mind. *See also* **somatic cell**. —**somatic** *adj.*

somat+ *a variant form of* **somato+** (before a vowel).

somatic cell any cell of an organism other than a germ cell.

somatic cell genetic disorder a category of genetic disorders in which defects are restricted to specific somatic cells, e.g. cancer cells. This contrasts with the other types of genetic disorder – single gene, multifactorial, and chromosome – in which the abnormality is present in all cells, including the germ cells.

somatic cell hybrid a hybrid cell formed from the fusion of different cells, usually from different species. Somatic cell hybrids obtained by the fusion of human and rodent cells are frequently used for gene mapping. *See* **cell fusion**.

somatic crossing over *an alternative name for* **mitotic recombination**.

somato+ *or (before a vowel)* **somat+** *comb. for* denoting the body, or soma.

somatocrinin *another name for* growth hormone releasing hormone (**GHRH**).

somatogenic **1** originating in the **soma** (def. 1), or body tissues. **2** of organic, rather than mental, origin.

somatoliberin *the recommended name for* growth hormone releasing hormone (**GHRH**).

somatomammotropin human chorionic somatomammotropin; *see* **choriomammotropin**.

somatomedin *generic name for* **insulin-like growth factors** (*abbr.*: IGF); in the human they comprise IGF-IA, IGF-IB, and IGF-II. Somatomedins were isolated on the basis of several properties: (a) activity on cartilage (incorporation of sulfate and thymidine), (b) insulin-like activity in adipose and muscle, and (c) mitogenic activity in cell culture. Somatomedin A is IGF-II, and somatomedin C is IGF-I (A and B). The term somatomedin should be used only when a generic term is needed, IGF-I (A or B) and IGF-II being used for the specific peptides. Somatomedin B is released from **vitronectin**, is a serum factor of unknown function, is increased in response to **somatotropin**, and has proteinase-inhibitory activity.

somatostatin *or* **somatotropin-release inhibiting factor** (*abbr.*: SRIF) *or (formerly)* **growth hormone-release inhibiting hormone** (*abbr.*: GH-RIH) a hypothalamic cyclic 14-residue peptide discovered as an inhibitor of the release of the pituitary growth hormone **somatotropin** and of the release of glucagon and insulin from the pancreas of fasted mammals; it also inhibits the release of gastrointestinal hormones and other secretory proteins. It has the sequence Ala-Gly-Cys-Lys-Asn-Phe-Phe-Trp-Lys-Thr-Phe-Thr-Ser-Cys, with a disulfide link

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between cysteines 3 and 14; this is called **somatostatin 14**. There also exists a bioactive 28-residue peptide – **somatostatin 28** – in which the 14-residue peptide is extended from the N terminus (the N-terminal residues are SANSNPALAPRERKAG–). Both forms are derived from the 92 amino-acid precursor, **prosomatostatin**, by tissue-specific proteolytic processing. Somatostatin is widely distributed, occurring not only in the central nervous system, but also in peripheral tissues such as stomach, intestine, and pancreas. It has diverse effects that are tissue specific, and can function as a neurotransmitter. Example (precursor) from human and *Macaca fascicularis* (a crab-eating monkey): database code SMS1_HUMAN, 116 amino acids (12.72 kDa). *See also* **somatostatin receptor**.

somatostatin receptor any of several membrane proteins that bind different forms of **somatostatin** and mediate its effects. Pharmacological studies indicate that there are at least two subtypes of receptor. In appropriate systems somatostatin suppresses receptor-induced stimulation of adenylate cyclase by activating the inhibitory **G-protein** G_i; it can decrease intracellular Ca^{2+} concentrations and inhibit the voltage-dependent current, I_{Ca}, by a G-protein-dependent cyclic AMP-independent mechanism. Somatostatin 14 enhances and somatostatin 28 reduces potassium current, I_K, also by G-protein-dependent cyclic AMP-independent mechanisms. There are several different types of somatostatin receptor; all are G-protein-coupled seven-transmembrane-domain proteins. The examples below are all from *Rattus norvegicus*. Type 1 has higher affinity for somatostatin 14 than 28 and is coupled to phosphotyrosine phosphatase and sodium–hydrogen-ion exchanger; example, database code SSR1_RAT, 391 amino acids (42.75 kDa). Types 2 and 3 are receptors for somatostatins 14 and 28 and inhibit adenylate cyclase; examples, database code SSR2_RAT, 369 amino acids (41.20 kDa) and database code SSR3_RAT, 428 amino acids (47.15 kDa). Type 4 is a receptor for somatostatin 14 and inhibits adenylate cyclase; example, database code SSR4_RAT, 384 amino acids (42.09 kDa). Type 5 is a receptor for somatostatin 28 and inhibits adenylate cyclase; example, database code SSR5_RAT, 363 amino acids (39.97 kDa). Hybridization studies indicate these are members of a larger family of somatostatin receptors; they are G-protein-coupled adenylate cyclase activators.

somatotrope *or* **somatotroph** a type of cell found in the lateral wings of the anterior pituitary and comprising about 50% of the hormone-producing cells of that part of the gland. Somatotropes are responsible for the production of **somatotropin**. Somatotrope adenomas cause **acromegaly**.

somatotroph *see* **somatotrope**.

somatotrophic **1** stimulating and maintaining the growth and development of any cell or tissue. **2** *(sometimes)* of or pertaining to **somatotropin**.

somatotropic **1** of, or relating to, **somatotropin**. **2** stimulating the mechanisms connected with growth or development of a cell or tissue. *Compare* **somatotrophic**.

somatotropic hormone *see* **somatotropin**.

somatotropin *or* **growth hormone** (*abbr.*: GH); *also called* **somatotropic hormone** (*abbr.*: STH); a hormone secreted by the anterior pituitary whose main effect is to stimulate growth. The human hormone (hGH) is mostly synthesized as the precursor of a single-chain, 191-residue protein, M_r 22 000, but 5–10% is a form of M_r 20 000 resulting from alternative splicing that deletes codons for amino acids 32–46 from the mRNA. Genes encoding hGH, **prolactin**, and **choriomammotropin** form a family with high nucleotide homology with five coding exons. Somatotropin secretion is pulsatile, especially during fasting, when cycles of about four hours' duration occur; it is stimulated by fasting or hypoglycemia, and hormonally by glucagon, GHRH, estrogens, and arginine vasopressin, and during the first phase of sleep; secretion is inhibited by hyperglycemia, somatostatin, the insulin-like growth factor IGF-I, and glucocorticoids. It is secreted from storage granules. *In vivo*, somatotropin tends to promote synthesis of protein, and lipolysis or reduced fat deposition, and growth and mitosis of cartilage. Deficiency leads to pituitary dwarfism types I and IV. Its actions *in vitro* include stimulation of amino-acid uptake in muscle, and lipolysis in adipose tissue, but many of its actions *in vivo* may depend on its action in stimulating synthesis and secretion of **somatomedins**. hGH has 85% homology with human choriomammotropin and 35% homology with human prolactin. Example (precursor) from human: database code SOMA_HUMAN, 217 amino acids (24.82 kDa). *See also* **GHRH**, **GHRH receptor**, **hypopituitarism**.

somatotropin-release inhibiting factor *abbr.*: SRIF; *an alternative name for* **somatostatin**.

somatrem methionyl human **somatotropin** (growth hormone); somatotropin with an additional N-terminal methionine. It results from the production of somatotropin using cDNA technology in bacterial clones; methionine is involved in the initiation of bacterial protein synthesis.

+some *comb. form* denoting body, esp. intracellular particle.

somite any of a series of paired blocks of mesoderm that form during early development in vertebrate embryos and lie on either side of the notochord. —**somital** *or* **somitic** *adj.*

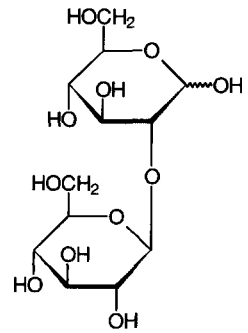
sonicate to expose any material or sample to ultrasonic pressure waves (at or around 20 kHz). The immersion of vessels in a water bath and their exposure to ultrasound is used as a means of cleaning (*see* **sonication bath**). The insertion of a **sonicator** probe into a vessel containing a suspension of membranes or other large assemblies causes their dispersion to smaller aggregates or assemblies.

sonication bath a water bath that is equipped with an oscillator, sited beneath the bowl, to produce ultrasound waves that permeate the water. It may be used for cleaning glass or other vessels or for degassing solvents.

sonicator a device that produces **ultrasonic** pressure waves. It usually consists of a stainless-steel rod, of diameter from 1–2 mm to about 2 cm, that is activated by an oscillator to produce ultrasound waves and is inserted into a vessel to **sonicate** a sample. *See also* **sonication bath**.

sonic hedgehog proteins analogues of **hedgehog protein** found in **zebrafish** and chickens and involved (in the latter case) in limb-bud pattern formation. The hedgehog proteins thus appear to be vital to pattern formation in several metazoan groups. The name sonic hedgehog is an allusion to a children's animated cartoon character.

sophorose the disaccharide 2-*O*-*β*-D-glucopyranosyl-D-glucose; it occurs in a glycoside of *Sophora japonica*.



sorbin a heat-stable peptide isolated from porcine intestine that increases water and sodium absorption in the intestine and gall-bladder. Example, database code SORB_PIG, 153 amino acids (17.46 kDa).

sorbitol *a nonsystematic name for* D-glucitol, one of the ten stereoisomeric hexitols. It can be derived from glucose chemically or metabolically (by NADPH-requiring aldehyde reductase; *other name*: aldose reductase, EC 1.1.1.21) by reduction of the aldehyde group, and is converted to D-fructose by L-idi-

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tol 2-dehydrogenase (EC 1.1.1.14). It is widely distributed in algae and higher plants, and was first discovered (1872) in the juice of berries from mountain ash (*Sorbus aucuparia*). It has a sweetening power about half that of sucrose, and is often used in sweeteners in conjunction with saccharin. Industrially it is of great importance in the food, pharmaceutical, paper, and textile industries. Its formation from excessive glucose concentrations in diabetics has been regarded as having pathological implications in lens tissue, which cannot convert it to fructose.

sorbose trivial name for the ketohexose *xylo*-2-hexulose; the enantiomer, L-sorbose, is present in fermented juice of mountain-ash berries, being formed by the bacterial oxidation of **sorbitol**. It is produced commercially by fermentation and used as an intermediate in the manufacture of **ascorbic acid**.

sorcin a protein, encoded in multidrug-resistant cells (*see* **MDR**), that binds calcium with high affinity. Example from human: database code SORC_HUMAN, 198 amino acids (21.68 kDa). *See also* **grancalcin**.

Soret band an absorption band at about 400 nm, characteristic of porphyrins. *See also* **cytochrome absorption bands**. [After Louis Soret (1827–90), Swiss physicist.]

sorocarp *see* ***Dictyostelium discoideum***.

sos *symbol for son of sevenless*, a gene encoding a guanine-nucleotide releasing protein involved in neuronal development in *Drosophila*. When coupled to the activated Sev receptor (*see* **Sevenless protein**) the *sos* product, Sos, mediates activation of *ras* by stimulating release of GDP, thereby promoting uptake of GTP. Database code SOS_DROME, 1595 amino acids (177.64 kDa).

SOS repair *or* **error-prone repair** a metabolic alarm system, occurring in bacteria, that helps the cell to save itself in the presence of potentially lethal stresses such as UV irradiation, thymine starvation, or the inactivation of genes essential for replication. Responses include mutagenesis, filamentation (cell elongation in the absence of division), activated excision repair, and activation of latent phage genomes. Mutagenesis occurs because under SOS conditions the gaps formed opposite **thymine dimers** can be filled by replication rather than by daughter-strand transfer. Replication of the dimer template is extremely inaccurate. The proteins involved include RecA protein (*see* ***recA***) and the products of two other RecA-inducible genes; expression is regulated by the ***lexA*** gene product.

Southern blotting a procedure for transferring denatured DNA from an agarose gel to a solid support membrane such as nitrocellulose or nylon. The procedure takes advantage of the property of nitrocellulose that it tenaciously binds single-stranded but not duplex DNA. The gel is soaked in 0.5 M NaOH, which converts the DNA to the single-stranded form. The gel is then overlaid with a sheet of nitrocellulose paper, which in turn is covered by a thick layer of paper towels and the entire assembly is compressed by a heavy weight. The liquid in the gel is forced (blotted) through the nitrocellulose so that the single-stranded DNA binds to it at the same position it had in the gel. The transfer to nitrocellulose can alternatively be accomplished by **electrophoretic transfer**. Nylon is now usually used in preference to nitrocellulose. DNA bands may be located using a radioactive or otherwise labelled probe. The name led to a nomenclature for other types of **blotting** (*see also* **Northern blotting**, **South-western blotting**, **Western blotting**). [After E. M. Southern (1938–), British molecular biologist.]

South-western blotting a technique in recombinant DNA technology for detecting plaques expressing **fusion proteins** where the foreign sequence encodes a DNA-binding protein that binds specifically to a particular DNA sequence. After treatment of the plaques to ensure release of the protein, **plaque-lift** is carried out onto a nitrocellulose (or other) **transfer membrane**, which is then incubated with a radiolabelled duplex DNA oligonucleotide that binds to the protein, which can then be detected by **autoradiography**. The term was derived by extension through the cardinal points from **Southern blotting**.

Soviet gramicidin *an alternative name for* **gramicidin S**.

Soxhlet extractor an apparatus for exhaustive extraction of soluble components from a sample of solid material by recycling a solvent through it, whereby solvent vapour from a boiler is continually condensed and the condensate allowed to percolate through the sample in a solvent-permeable thimble, from which it is returned, usually periodically via a siphon, to the boiler, where the eluted substances accumulate. [After Franz Soxhlet (1848–1926), Belgian chemist, who devised it.]

soybean *or (esp. Brit.)* **soya bean** a leguminous plant, *Glycine max*, originating in China (known from at least 2500 BC) and now cultivated widely in Asia, Europe, and America for forage and for its seeds. The bean has an oil content of 18–22%, and is also rich in protein — soybean protein is used as a human food and is the basis of tofu. *See also* **soybean oil**, **soybean trypsin inhibitor**.

soybean oil an edible oil obtained from the seeds of the soybean plant and valued for its high content of linoleic acid. The composition is typically as follows: 18:2 ω6, 44–62%; 18:3 ω3, 4–11%; 18:1 ω9, 19–30%; 16:0, 7–14%.

soybean trypsin inhibitor *abbr.*: STI; either of two different types of trypsin inhibitor, the Bowman–Birk and the Kunitz inhibitors. Both have given their names to a class of proteinase inhibitor. The two soybean inhibitors differ markedly from each other in size, structure, and properties. The **Bowman–Birk inhibitor** is a 71 amino-acid, 7.873 kDa protein: database code IBB1_SOYBN. It has seven disulfide bridges. There are two active sites, one specific for trypsin and the other for chymotrypsin. Bowman–Birk type inhibitors are found in many cereals and legumes, and ancestrally may represent storage proteins. The **soybean Kunitz inhibitors** comprise three allelic proteins, A, B, and C, together with two Kunitz-type trypsin inhibitors, named KTI1 and KTI2. The A, B, and C proteins have 181 amino acids (20 kDa): database code (of A and C) ITRA_SOYBN. They have two disulfide bonds. They are heat-stable and resistant to proteases, and form a 1:1 stoichiometric complex with trypsin, that is highly stable (K_a 5×10^9). They inhibit chymotrypsin to a much smaller degree and are inactive against other endopeptidases, but modification of Arg^{63} to Trp converts them to strong chymotrypsin inhibitors with little action on trypsin. The Kunitz family of inhibitors embraces trypsin, chymotrypsin, cathepsin D, and subtilisin inhibitors (*see* **Kunitz inhibitor**).

sp *abbr. for* synperiplanar; *see* **conformation**.

sp. (*pl.* **spp.**) *abbr. for* species (singular).

Sp *abbr. for* isomer of a thionucleotide.

SP *abbr. for* **1** secretory piece. **2** substance P.

SP-1 *abbr. for* secretory protein 1.

[S]pA *symbol for* adenosine 5′-thiophosphate (alternative to Ado*P*[S].

space *or* **volume of distribution** (*in tracer kinetics*) an apparent volume obtained as the amount of radioactivity retained divided by the concentration of the tracer in the plasma. The concept of space has the limitations discussed under **apparent exchangeable mass**. *See also* **compartment**.

spacer **1** *(in molecular biology)* a sequence of bases of unknown function occurring in a DNA molecule and lying between sequences of transcribed DNA; spacer DNA is not usually transcribed. The term has also been used to refer to some stretches of **primary transcript**, e.g. a region in the mammalian primary transcript for rRNA, lying between 18S RNA and 28S RNA, that is not found in mature rRNA. **2** *(in chromatography) an alternative term for* **spacer arm**.

spacer arm *or* **spacer** the (usually) hydrocarbon chain interposed, by covalent linkages, between the specific ligand and the supporting matrix in **affinity chromatography**.

spacer gel *(in electrophoresis)* a small section of gel, polymerized above a polyacrylamide (or other) resolving gel, that lacks resolving power and serves to concentrate the material being electrophoresed as a tight band at the top of the resolving gel.

SPARC *abbr. for* secreted protein acidic and rich in cysteine; *also called* **osteonectin**; a protein expressed in cells of tissues

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undergoing morphogenesis or wound repair and secreted into the basement membrane, where it interacts with other proteins, e.g. collagen and thrombospondin, and appears to have a role in regulating cell growth. It contains an **EF-hand** that binds one calcium ion and an acidic region that binds other calcium ions more loosely. Example from human (precursor): database code SPRC_HUMAN, 303 amino acids (34.63 kDa).

spare receptors receptors that are in excess of those required to evoke a given response to a drug, hormone, or other agonist. For a given agonist, the size of the population of spare receptors (**receptor reserve**) can vary with the tissue and with the magnitude of the response being measured. For different drugs, the receptor reserve varies with drug efficacy.

sparging the bubbling of gas into a liquid medium. This technique may be applied to fermenters to introduce air directly into a culture, or it may be used to replace one dissolved gas by another, e.g. in displacing oxygen with an inert gas in liquid chromatography solvents.

spatula a (usually) small, flattened, sometimes curved, utensil made of metal (often stainless steel), bone, or wood and used to dispense crystalline or powdered material.

Spd *abbr. for* sphingoid.

species (*pl.* **species**) *abbr.*: sp. (*sing.*) *or* spp. (*pl.*); a fundamental taxonomic category ranking below a genus and consisting of a group of closely related individuals that can interbreed freely to produce fertile offspring.

species-specific confined to the one or several species referred to.

specific **1** relating to a particular or specified thing. **2** (as a modifier of certain quantitative terms) indicating a relationship of the quantity to mass and dimension in terms of standard (now normally SI) units; e.g. **specific catalytic activity**, **specific enzyme activity**, **specific optical rotation**. **3** of, or relating to, a **species**. *See also* **specificity**.

specific acid catalysis a **homogeneous catalysis** in which the catalysts are free hydrons, H^+ (or hydronium ions, H_3O^+). The catalysis is not affected by other acidic species present. *Compare* **general acid-catalysis**.

specific activity the **activity** (def. 1, 2) of, e.g., a radionuclide or an enzyme, expressed as a function of mass.

specifically labelled describing an isotopically labelled compound in which both the position of labelling and the number of labelling nuclides at that position are known. Such a molecule is designated by a convention exemplified by $CH[^2H_2]-CH_2-O[^2H]$.

specific base catalysis a **homogeneous catalysis** in which the catalysts are hydroxide ions, OH^-. The catalysis is not affected by other basic species present. *Compare* **general base-catalysis**.

specific catalytic activity the **catalytic activity** of an enzyme under specified conditions divided by the mass of an enzyme or enzyme preparation. It is a quantity useful for denoting the extent of purification of an enzyme; it may be expressed in katals per kilogram.

specific dynamic action the increase in heat production above the basal level that occurs in animals after the ingestion of food, particularly of protein.

specific enzymic activity the phenomenological coefficient that relates **enzymic activity** under specified conditions to the mass of an enzyme or enzyme preparation. It may be expressed in katals per kilogram of protein. Now obsolete, it has been superseded by **specific catalytic activity**. *Compare* **molar enzymic activity**.

specific gravity *a former name for* **relative density**.

specific heat capacity *symbol*: c_p (at constant pressure) *or* c_v (at constant volume); the quantity of **heat** required to raise the **temperature** of unit mass of a substance by one degree. It is expressed (usually) in $J\ K^{-1}\ kg^{-1}$.

specificity an index of the degree to which an association between two molecular units or assemblies may be considered unique; in many applications it is judged by the magnitude of an effect (enzyme–substrate, ligand–receptor interaction, or drug action). It is quantified in suitable units under defined conditions, in relation to the magnitude of effect of other substances with similar action, amplified by studies made when the substance under consideration is in a direct competitive interaction with other such substances. The success of other substances in competing with the subject of study is normally quantified by kinetic analysis (*see* **competitive inhibition**). The problem of quantifying specificity may be examined by referring to **specificity constant**.

specificity constant the ratio of the catalytic constant, k_{cat}, to the Michaelis constant, K_m. It can aid in comparing the activity of an enzyme in its action on different substrates. From **Michaelis kinetics**, using the Michaelis–Menten equation,

$$v = (k_{cat}/K_m)[E]_o[S]$$

when [S] is very small (since then, little enzyme has bound substrate, so $[E] \approx [E]_o$, and [S] can be neglected in relation to K_m). Thus for substrate A,

$$v_a = (k_{cat}/K_m)_A[E]_o[A],$$

and for substrate B,

$$v_b = (k_{cat}/K_m)_B[E]_o[B].$$

So

$$v_a/v_b = \{(k_{cat}/K_m)_A \times [A]\}/\{(k_{cat}/K_m)_B \times [B]\},$$

and, at the same substrate concentrations, the activity of the enzyme against the different substrates reduces to a comparison of the respective specificity constants (k_{cat}/K_m); K_m is not of itself a sufficient index of specificity.

specific optical rotation *symbol* $[\alpha]^\theta_\lambda$; the optical rotation of light of a specified wavelength (or frequency) achieved by a solution at a specified temperature. It is given by the relation $[\alpha]^\theta_\lambda = \alpha/l\rho$ where α is the observed rotation in degrees, l is the length of the sample tube (in dm), ρ is the density of the liquid (in $g\ mL^{-1}$), λ is the wavelength of the light (or other electromagnetic radiation) used, and θ is the Celsius temperature. For a solution of concentration c (in g solute per 100 mL solution), $[\alpha]^\theta_\lambda = \alpha/lc$ in degrees $dm^2\ g^{-1}$. *Compare* **molecular optical rotation**.

specific refractivity *see* **refractivity**.

specific viscosity *symbol*: η_{sp}; the fractional change in **viscosity** produced by adding a solute to a solvent. It is given by the equation:

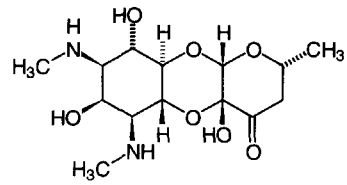
$$\eta_{sp} = (\eta/\eta_0) - 1 = Avc + Bv^2c^2 + Cv^3c^3 + \ldots\ldots$$

where η_0 is the viscosity of the solvent, η is the intrinsic viscosity of the solution, A, B, and C are shape-dependent constants, c is the concentration of the solute, and v is the specific volume of one solute molecule.

specific volume *symbol*: v; for a pure substance, the volume, V, of a sample, divided by the mass, m, of the sample; $v = V/m = 1/\rho$, where ρ is the **mass density** of the substance. The SI unit is $m^3\ kg^{-1}$. *See also* **partial specific volume**.

'specifier' protein a protein that, when it combines with an enzyme or enzyme–substrate, modifies the catalytic specificity of the system. An example is α-lactalbumin, which modifies the substrate (acceptor) specificity of *N*-acetyllactosamine synthase (EC 2.4.1.90; *other name*: UDPgalactose:*N*-acetylglucosamine β-D-galactosyltransferase) from *N*-acetylglucosamine to glucose.

spectinomycin an aminocyclitol antibiotic found in the growth medium of *Streptomyces spectabilis*. It has a wide



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range of activity against Gram-negative bacteria, with a more selective activity against Gram-positive bacteria. It is highly active against *Neisseria gonorrhoeae*. It inhibits protein synthesis by binding to the bacterial 30S ribosomal subunit.

spectra the plural of **spectrum**.

spectrin a protein that is the major constituent of the erythrocyte cytoskeletal network. It associates with band 4.1 (*see* **band protein**) and **actin** to form the cytoskeletal superstructure of the erythrocyte plasma membrane. It is composed of nonhomologous chains, α and β, which aggregate side-to-side in an antiparallel fashion to form dimers, tetramers, and higher polymers. Anchorage to the cytoplasmic face of the plasma membrane is mediated by another protein, **ankyrin**, which links β spectrin to transmembrane protein band 3, and by the binding of band 4.1 to **glycophorin**. Interaction between spectrin and other proteins is thought to be responsible for the maintenance of the biconcave shape of human erythrocytes, for the regulation of plasma membrane components, and for the maintenance of the lipid asymmetry of the plasma membrane. Spectrin-like proteins have five domains. Example from human, α chain: database code SPCA_HUMAN, 2429 amino acids (280.74 kDa); β chain: database code SPCB_HUMAN, 2137 amino acids (246.04 kDa).

spectrofluorometer an instrument used for measuring the **fluorescence** emitted by compounds excited by incident radiation produced within the instrument. The excitation radiation is produced by a lamp, and filters or diffraction grating monochromators are employed to isolate both the incident and emitted radiation to narrow wavebands. The emitted radiation is detected by photomultipliers.

spectrogram a photographic record of a **spectrum** produced by a **spectrograph**.

spectrograph a **spectrometer** or **spectroscope** with a facility for producing a photographic record of the spectrum under consideration. *Compare* **spectroscope**. —**spectrographic** *adj.*; **spectrographically** *adv.*; **spectrography** *n.*

spectrometer any instrument used to produce and examine a **spectrum**, such as a **spectrophotometer** or a **spectroscope**. —**spectrometric** *adj.*; **spectrometry** *n.*

spectrophotometer an apparatus to measure the proportion of the incident light (or other electromagnetic radiation) absorbed (or transmitted) by a substance or solution at each wavelength of the spectrum. —**spectrophotometric** *adj.*; **spectrophotometry** *n.*

spectroscope an instrument for studying spectra, either qualitatively or quantitatively. —**spectroscopic** *or* **spectroscopical** *adj.*; **spectroscopically** *adv.*

spectroscopy the investigation of the chemical composition, molecular structure, or atomic structure of a substance or solution by observation of its interaction with electromagnetic radiation using a spectroscope.

spectrum (*pl.* **spectra**) *(in physics)* an arrangement of the components of a complex electromagnetic radiation (light, etc.) or sound in order of frequency or energy, thereby showing a distribution of energy among the components. —**spectral** *adj.*

Spemann's organizer an embryonic signalling centre located in the dorsal lip of the blastopore. It plays a crucial role in the organization of the formation of the main body axis of a developing embryo. [After Hans Spemann (1869–1941), German zoologist and embryologist.]

spermaceti *or* **cetaceum** a white, translucent, waxy solid, m.p. 42–50 °C, consisting mainly of the ester cetyl palmitate and obtained from oil in the head of the sperm whale (*Physeter catodon*) and related cetaceans. It is used in the manufacture of cosmetics, ointments, soaps, etc.

spermadhesin *or* **AQN1** a secretory protein of male accessory glands that is found on the sperm surface and mediates sperm binding to the zona pellucida. Example from *Sus scrofa*: database code AQN1_PIG, 111 amino acids (11.88 kDa).

spermatogenesis the formation of spermatozoa in the male reproductive system. The sperms are formed from male germ cells, **spermatogonia**, which line the inner wall of the seminiferous tubules in the testis. A single spermatogonium divides by mitosis to form **primary spermatocytes**, each of which undergoes the initial division of meiosis to form two **secondary spermatocytes**. Each of these then undergoes the second meiotic division to form two **spermatids**, which mature into spermatozoa without further cell division by a process called **spermiogenesis**. All these cell types are nourished and supported by neighbouring **Sertoli cells**. Spermatogenesis also requires the presence of testosterone-secreting **Leydig cells**.

spermidine *N*-(3-aminopropyl)-1,4-diaminobutane; $NH_2(CH_2)_3NH(CH_2)_4NH_2$; one of the polyamines.

spermidine synthase EC 2.5.1.16; *other names*: putrescine aminopropyltransferase; aminopropyl-transferase; an enzyme that catalyses the formation of **spermidine** from *S*-adenosylmethioninamine and putrescine with formation of 5′-methylthioadenosine. Example from human: database code SPEE_HUMAN, 302 amino acids (33.79 kDa).

spermine *N*,*N*-bis(3-aminopropyl)-1,4-diaminobutane; $NH_2(CH_2)_3NH(CH_2)_4NH(CH_2)_3NH_2$; one of the polyamines.

spermine synthase EC 2.5.1.22; *other name*: spermidine aminopropyltransferase; an enzyme that catalyses the formation of **spermine** from *S*-adenosylmethioninamine and spermidine with formation of 5′-methylthioadenosine.

sperm tail *see* **cilium**.

SPF *abbr. for* specific-pathogen-free.

Sph *symbol for* sphingosine.

S phase the phase of the eukaryotic cell cycle in which DNA is synthesized. *See* **cell-division cycle**.

spherocyte a rounded red blood cell that has lost its normal biconcave shape owing to damage to the surface membrane or to some disorder of metabolism. Spherocytes appear smaller and darker than normal red cells.

spherocytosis the condition of having **spherocytes** in the blood.

spheroid **1** a solid figure that is similar to but not identical with a sphere. **2** an **ellipsoid of rotation**, especially one in which the major axis of its parent ellipse is only slightly longer than its minor axis. —**spheroidal** *adj.*

spheroplast the globular form of a bacterial cell in which the cell-wall structure has been modified (e.g. by growth in the presence of penicillin) rather than totally removed. The term also denotes a form of yeast cell obtained by partial hydrolysis of the cell wall. A prefix may be used to indicate the method of induction, e.g. penicillin-spheroplast. *Compare* **protoplast**.

spherosome an organelle, generally spherical or oblate and 0.4–3 μm in diameter, that occurs in lipid-storage tissues in plants, e.g. endosperm of castor-bean seeds. The nature of the surrounding membrane is still in doubt.

sphinganine D-*erythro*-2-amino-1,3-octadecanediol; D-*erythro*-dihydrosphingosine; the metabolic precursor of **sphingosine**. It is formed from palmitoyl-CoA and serine by, first, the action of **serine *C*-palmitoyltransferase**, which forms 3-dehydro-D-sphinganine, which is then reduced to sphinganine by 3-dehydrosphinganine reductase, EC 1.1.1.102. *See also* **sphingolipids**, **sphingoid**.

sphingoid *or* **sphingoid base** *symbol*: Spd; any of a class of compounds comprising **sphinganine** and its homologues and stereoisomers, and derivatives of these compounds.

sphingolipid any of a class of lipids containing the long-chain amino diol, **sphingosine**, or a closely related base (i.e. a **sphingoid**). A fatty acid is bound in an amide linkage to the amino group and the terminal hydroxyl may be linked to a number of residues such as a phosphate ester or a carbohydrate. The predominant base in animals is sphingosine while in plants it is **phytosphingosine**. The main classes are: (1) phosphosphingolipids (also known as sphingophospholipids), of which the main representative is **sphingomyelin**; and (2) **glycosphingolipids**, which contain at least one monosaccharide and a sphingoid, and include the **cerebrosides** and **gangliosides**. Sphingolipids play an important structural role in cell membranes, and may be involved in the regulation of protein kinase C.

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sphingolipid activator proteins *see* **saposins**.

sphingolipidosis (*pl.* **sphingolipidoses**) any of several inherited pathological conditions in humans in which one or more sphingolipids accumulate in the tissues because of a deficiency of the corresponding degradative enzyme. They include **ceramidase** deficiency, **Fabry's disease**, **galactosylceramide lipidosis**, G_{M1} and G_{M2} **gangliosidoses**, **Gaucher's disease**, **metachromatic leukodystrophy**, and **sphingomyelin lipidosis**.

sphingomyelin *N*-acyl-4-sphingenyl-1-*O*-phosphorylcholine; any of a class of phospholipids in which the amino group of **sphingosine** is in amide linkage with one of several fatty acids, mostly C_{20} or higher and either saturated or monounsaturated, while the terminal hydroxyl group of sphingosine is esterified to phosphorylcholine. Sphingomyelins are found in large amounts in brain and other nervous tissue. They do not occur in plants.

sphingomyelin lipidosis *or* **Niemann–Pick disease** a genetic disease of humans in which **sphingomyelin** accumulates in the tissues due to a deficiency of the enzyme **sphingomyelin phosphodiesterase**. It is associated with mental retardation.

sphingomyelin phosphodiesterase EC 3.1.4.12; *other names*: acid sphingomyelinase; neutral sphingomyelinase; a lysosomal enzyme that catalyses the hydrolysis of sphingomyelin to *N*-acylsphingosine and choline phosphate. Deficiency of the enzyme is the cause of Niemann–Pick disease (**sphingomyelin lipidosis**), in which there is an accumulation of sphingomyelin. Example (precursor) from human: database code ASM_HUMAN, 629 amino acids (69.78 kDa).

sphingophospholipid *see* **sphingolipid**.

sphingosine *symbol*: Sph; *trans*-D-*erythro*-2-amino-4-octadecene-1,3-diol; $CH_3(CH_2)_{12}CH{=}CH{-}CHOH{-}CHNH_2{-}CH_2OH$; a long-chain amino diol sphingoid base that occurs in most **sphingolipids** of animal tissues. *See also* **phytosphingosine**.

sphingosine *N*-acyltransferase EC 2.3.1.24; an enzyme of the pathway for synthesis of sphingolipids that catalyses the acylation of sphingosine by acyl-CoA to form *N*-acylsphingosine (ceramide) and CoA.

spicule a roughly cone-shaped structure or tissue element, such as that projecting from the membrane of a red blood cell. Calcareous or siliceous spicules are found in the skeletons of sponges and corals.

spin *(in physics)* **1** the quantized angular momentum of an elementary particle, in the absence of orbital motion. **2** the quantized angular momentum of an atomic nucleus, including contributions from the orbital motions of nucleons. **3** the quantized angular momentum of an electron that adds to the orbital angular momentum, thus producing fine structure in line spectra.

spinal cord the part of the central nervous system that is enclosed in the vertebral column. Its function is to connect the innervation of most parts of the body via the spinal nerves to the brain.

spinal nerves the pairs of nerves that arise from the spinal cord and are distributed to various peripheral parts of the body. In humans there are 31 pairs.

spin coupling *or* **spin–spin coupling** (*in nuclear magnetic resonance spectroscopy*) the influence of one nucleus on another, such that the nuclear spin of one nucleus is coupled via the bonding electrons to the coupled nucleus, which experiences two different microenvironments and thus resonates at two slightly different frequencies. This results in the splitting of the resonance line into two lines (a doublet).

spin density the fraction of unpaired electron spin that is in the vicinity of a given atomic nucleus in a molecule.

spindle the array of microtubules and associated molecules that forms between the opposite poles of a eukaryotic cell during mitosis or meiosis and serves to move the duplicated chromosomes apart. During mitosis the spindle starts to form outside the nucleus while the chromosomes are condensing during prophase. At the start of M phase, the two **centrosomes** that have been formed move to opposite sides of the nucleus, and form the two poles of the mitotic spindle. Microtubules grow away from the centrosomes towards the chromosomes, the minus ends being attached to the centrosome, and the plus ends growing towards the **kinetochore**. These microtubules eventually bind to kinetochores and are thus known as kinetochore microtubules. Other microtubules, known as polar microtubules, grow towards the chromosomal region, but eventually bind directly to other polar microtubules growing from the opposite centrosome. These push the poles of the spindle apart. Each centrosome eventually becomes attached through the kinetochore microtubules to one of the sister chromatids of each chromosome, and pulls these away to effect the chromatid separation that occurs at anaphase. A similar series of events occurs at the corresponding phases of meiosis.

spin hamiltonian a formulation in **quantum mechanics** used in the determination of the energy levels of the spin of an electron or a nucleus in **electron spin resonance spectroscopy** or, less commonly, in **nuclear magnetic resonance spectroscopy**. *See also* **Hamiltonian operator**.

spin immunoassay *or* **free-radical assay technique (of immunoassay)** (*abbr.*: FRAT) a technique in which a **spin label** is attached to a specimen of the substance to be assayed and an antibody is raised against the substance. On mixing the antibody with the labelled substance there is a change in the electron spin resonance (ESR) spectrum because of the inhibition of tumbling caused by the antibody 'immobilizing' the labelled substance. On adding some of the unlabelled substance there is competition for the antibody, and the changes in the ESR spectrum are partially reversed to an extent dependent on the concentration of the added, unlabelled, substance.

spin label **1** a synthetic paramagnetic organic free radical, usually having a molecular structure and/or chemical reactivity that facilitates its attachment or incorporation at some particular target site in a macromolecule, or assemblage of macromolecules. **2 spin-label** to effect labelling of a substance or structure with a spin label (def. 1).

spin-lattice relaxation time *or* **longitudinal relaxation time** *(in nuclear magnetic resonance spectroscopy) symbol*: T_1; the time taken for the upper electron spin state to dissipate its excess energy. Its reciprocal is the spin-lattice relaxation rate (*see* **correlation time**).

spinner culture the culture of cells in bottles or tubes that are continuously rotated.

spin polarization *or* **spin polarisation** a phenomenon in which the unpaired electron spin on one atom or part of a molecule is transferred to another atom, brought about by interaction between the unpaired electron on the first atom and the paired electrons on the second atom (which lacks unpaired electrons) causing one of the paired electrons to have a lower energy than the other. *See also* **chemically induced dynamic nuclear polarization**.

spin–spin broadening an increase in line width in **electron spin resonance spectroscopy**, caused by interactions between neighbouring dipoles.

spin–spin coupling *see* **spin coupling**.

spin–spin coupling constant *(in nuclear magnetic resonance spectroscopy)* a measure of the specific interaction of one nucleus with another that gives rise to a splitting of the resonance bands produced by each nucleus.

spin–spin splitting splitting in the lines of a **nuclear magnetic resonance** spectrum brought about by the interaction of the magnetic moment of the nucleus of a given atom in a molecule with those of neighbouring nuclei. It is used in the assignment of particular nuclear resonances and in the determination of molecular conformations. *See also* **hyperfine splitting**.

spin state the orientation, in a strong magnetic field, of an unpaired electron or nuclear spin, e.g. parallel or antiparallel to the field direction.

spin trapping a technique in which a reactive free radical is

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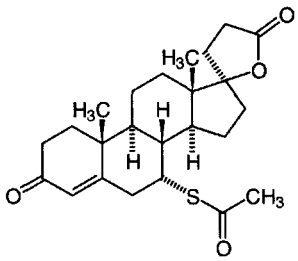
trapped by an addition reaction to produce a more stable radical, detectable by **electron spin resonance spectroscopy**, whose hyperfine coupling parameters permit identification of the initial radical trapped.

spiro compound any compound containing two rings joined by one common atom, designated the **spiro atom**, as in the case of the γ-lactone ring of **spironolactone**.

spironolactone 7-(acetylthio)-17-hydroxy-3-oxo-pregn-4-ene-21-carboxylic acid γ-lactone; a synthetic steroid lactone that is used as a diuretic. It is structurally similar to **aldosterone**, and competitively inhibits the renal tubular action of this hormone. It is metabolized to canrenone, the active compound, by removal of the acetylthio group and insertion of a 6,7 double bond.



spleen exonuclease *see* **phosphodiesterase II**.

splenin *see* **thymopoietin**.

splenopentin a synthetic peptide that corresponds to residues 32–36 of splenin (*see* **thymopoietin**).

spliceosome a **ribonucleoprotein** complex, containing RNA and **small nuclear ribonucleoproteins** (snRNPs) that is assembled during the **splicing** of the messenger RNA **primary transcript** to excise an **intron**. snRNPs designated U1, U2, U4, U5, and U6 are variously involved; U1 may bind the GU consensus sequence of the 5′ **splice site** and U5 with U4/U6 probably binds to the 3′ splice site consensus sequence, AG. U2 may be part of a component binding the UACUA[A]C consensus sequence ([A] is invariant) at a site slightly upstream from the 3′ splice site, known as the branch site. The mechanism appears to involve cutting at the 5′ side of the GU consensus sequence, which curls back to form a G5′–2′A bond with the invariant A of UACUA[A]C. This linkage generates the loop of the so-called **lariat**. Cutting out the 3′ splice site follows on the 3′ side of AG to release the complete intron (in the form of the lariat), and the cut ends of the exons are then ligated.

splice site the sequence of bases at each end of an **intron** that determines the point of **splicing**. The 5′ splice site (site at the 5′ end of the intron) is termed the donor site, consensus sequence GU, while the 3′ splice site is termed the acceptor, consensus sequence AG.

splicing **1** (of DNA) the covalent linkage, by the action of a **DNA ligase** (EC 6.5.1.1, requires ATP, or EC 6.5.1.2, requires NAD^+), of two fragments of duplex DNA at complementary single-stranded terminations. **2** (of RNA) the enzymic process in eukaryotic cells by which **introns** are excised from heterogeneous nuclear RNA (hnRNA) following its transcription from DNA, and the cut ends are rejoined to form messenger RNA (mRNA), in which the message is continuous, before its translation into polypeptide. In yeast, the splicing of transfer RNA involves cutting at the splicing junctions by an endonuclease followed by a process involving ATP whereby the two exon sequences are joined. Group I mitochondrial RNA is spliced by an autocatalytic mechanism, the RNA itself having the ability to catalyse its own splicing; nuclear mRNA precursor – the primary transcript – is spliced by a complex assembly incorporating snRNP and called a **spliceosome**; it involves the formation of a **lariat**. Splicing of group II mitochondrial RNA also involves the formation of a lariat but without formation of a spliceosome. Splicing in which the cut ends are joined directly within the same RNA molecule is called ***cis*-splicing**; ***trans*-splicing** refers to situations in which the cut end from the splicing site rejoins to a splicing site on another RNA molecule. **3** (of protein) a post-translational modification of protein that includes two concerted proteolytic cleavages and one ligation that results in excision of an inner sequence of the original polypeptide chain to form one protein, and ligation of the two outer sequences to form a second protein. It is thought to be an autocatalytic process. The excised inner sequence is known as an **intein**, the ligated outer sequences as an **extein**. *See also* **gene splicing**.

splicing factor 2 *abbr.*: SF2; a protein, present in nuclear extracts, that functions in an early step in splicing pre-mRNA. It is resistant to mild heat treatment, but inactivated by *N*-ethylmaleimide. It consists of two peptides, P32 and P33, and is involved in ensuring accuracy of splicing. Example, P32 from human: database code SP32_HUMAN, 282 amino acids (31.36 kDa). *See also* **pre-mRNA processing protein**.

split gene a gene that is not represented by a continuous DNA sequence; an interrupted gene.

spoke protein a protein associated with the filamentous structure of kinetochore microtubules in the mitotic spindle. Soluble and cytoplasmically localized during interphase, it becomes primarily associated with the mitotic spindle in mitosis. Example, spoke protein 4 (of five different ones) from *Chlamydomonas reinhardtii*: database code RSP4_CHLRE, 465 amino acids (49.74 kDa).

spongiform encephalopathy any of a group of diseases of human and other animals characterized by the presence of many vacuoles in brain tissue, giving it a spongy appearance. The group includes **bovine spongiform encephalopathy, scrapie** in sheep, and **Creutzfeldt–Jakob disease, Gerstmann–Straussler syndrome**, and **kuru** in humans. *See also* **prion, prion protein**.

spontaneous generation *see* **abiogenesis**.

spontaneous hypoglycemia *see* **glycemia**.

spore a small, often microscopic, reproductive unit consisting of one or several cells. Spores are produced by fungi, bacteria, certain plants, and protozoa. They may variously serve as a means of rapid vegetative propagation, or as a dormant stage in the organism's life cycle. Spores have very low metabolic activity and give rise to a vegetative cell upon germination; they are usually more heat resistant than vegetative cells and are adapted for dispersal. Spores may be sexual or asexual.

sporulation the formation of **spores**.

spot **1** *(in chemistry) or* **spot test** to test for a substance by applying a small amount of detection reagent to a surface. **2** *(in molecular biology)* to detect, using radioactive oligonucleotide probes, oligonucleotides applied in spots onto hybridization filters (**spot blots**).

spoT a gene in *Escherichia coli* for the enzyme guanosine-3′,5′-bis(diphosphate) 3′-pyrophosphohydrolase; EC 3.1.7.2; *other name*: (ppGpp)ase; it catalyses the hydrolysis of guanosine 3′,5′-bis(diphosphate) to guanosine 5′-diphosphate and pyrophosphate. The SpoT protein cycles ppGpp formed as a part of the **stringent response**. The name is jocular, ppGpp and pppGpp originally having been referred to as 'magic spot nucleotides'. Example from *E. coli*: SPOT_ECOLI, 702 amino acids (79.34 kDa). *See also* ***relA***, **stringent factor**.

spp. *abbr. for* species (plural).

SPP-1 *see* **osteopontin**.

[S]ppA *symbol for* adenosine 5′-β-thiodiphosphate (alternative to Ado*PP*[S]).

[S]pppA *symbol for* adenosine 5′-γ-thiotriphosphate (alternative to Ado*PPP*[S]).

spreading factor *see* **hyaluronidase**.

SQDG *abbr. for* sulfoquinovosyldiacylglycerol (*see* **sulfonolipid**).

SQL *abbr. for* symbolic query language; a **query language** used with related databases, e.g. **SYBASE**. It is often pronounced 'sequel'.

squalamine a water-soluble aminosterol isolated from the

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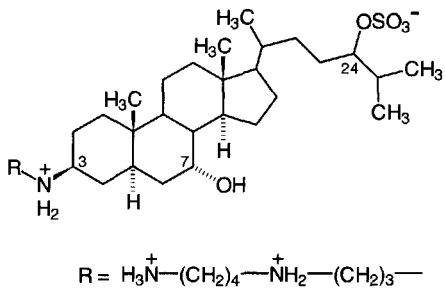
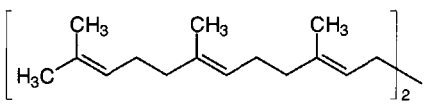
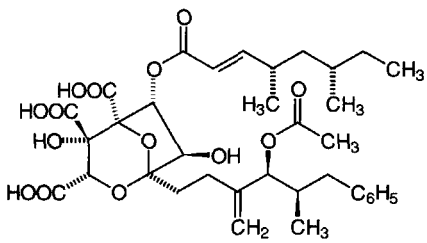
dogfish shark, *Squalus acanthias*. It has antibiotic properties against Gram-negative and Gram-positive bacteria and protozoa. It is an adduct of **spermidine** and a sulfate bile salt.



squalene 2,6,10,15,19,23-hexamethyl-2,6,10,14,18,22-tetracosahexaene; the linear triterpene precursor of all cyclic triterpenoids and the sterols. Although first isolated from shark-liver oils and later found in many other fish-liver and plant oils, squalene is widely distributed in plant and animal cells as a metabolic intermediate. It is formed from acetyl-CoA, via a pathway whose intermediates include **mevalonate**, **isopentenyl diphosphate**, **geranyl diphosphate**, and farnesyl diphosphate. The latter is converted to presqualene diphosphate, which is then reduced to squalene by NADPH with loss of pyrophosphate; both steps are catalysed by **farnesyltransferase**. [From Latin *squalus*, marine fish, later specifically used to mean shark.]



squalestatin a fermentation product of *Coelomycete* spp. that is a potent selective inhibitor of squalene synthase, and lowers serum cholesterol *in vivo*.



squalestatin 1

sr *symbol for* steradian.
Sr *symbol for* strontium.
SR *abbr. for* sarcoplasmic reticulum.
src an oncogene (v-*src*), originally discovered in the Rous sarcoma virus, the product of which is pp60$^{v\text{-}src}$, a 60 kDa protein that undergoes phosphorylation/dephosphorylation. A normal cellular gene (or **protooncogene**), c-*src*, codes for a related protein; both proteins have **tyrosine kinase** activity. The viral oncogene product and its normal counterpart differ in amino-acid residues, especially at the C terminus where the last 19 residues of pp60$^{c\text{-}src}$ are replaced by 12 other residues in pp60$^{v\text{-}src}$. The Src family of tyrosine kinases is the largest of the nonreceptor tyrosine kinase families and is formed from a group of proteins that all share a high homology with the oncoprotein, v-Src, and the cellular counterpart, c-Src. Members of the Src family include Src, Yes, Fyn (*see* ***FYN***), Lck (*see* ***LCK***), Lyn (*see* ***lyn***), Blk (*see* ***blk***), Hck, Fgr (*see* ***FGR***), and Yrk, which range in size from 53 to 64 kDa. They all share a number of features including an N-terminal myristoylation site (a mechanism for promoting their association with membranes), a unique domain, two conserved segments known as Src homology 2 domain (SH2 domain) and Src homology 3 domain (SH3 domain(*see* **SH domain**)), a tyrosine kinase domain, and a C-terminal regulatory domain. In vertebrates, the kinase activity of Src family members is normally inhibited by the phosphorylation of a tyrosine residue within the kinase domain. In v-*src* the region of the gene encoding the negative regulatory C-terminal tyrosine has been deleted, leading to v-Src having a higher constitutive tyrosine kinase activity than c-Src. Other mutations associated with oncogenic activation map to the SH2 and SH3 domains, supporting the proposal that in the resting cell Src is kept in an inactive state by the binding of its SH2 domain to the phosphotyrosine residue in its negative regulatory domain so keeping the kinase in an inactive conformation. SH3 domains may participate in this repression, possibly by binding proline-rich regions in the kinase domain. Activation of Src family members occurs by two potential mechanisms: (1) the co-presence of another protein containing a specific phosphotyrosine residue that has a higher affinity for the SH2 domain than the negative regulatory phosphotyrosine within the Src member; or (2) the dephosphorylation of the negative regulatory phosphotyrosine by a specific protein tyrosine phosphatase. Example from human: database code KSRC_HUMAN, 536 amino acids (59.77 kDa).
Src homology domain *see* **SH domain**.
Srd *symbol for* a residue of the ribonucleoside thiouridine (when the position of the thiol group in its thiouracil moiety is unknown or unspecified; alternative to S or sU).
SRE *abbr. for* serum response element.
SRF *abbr. for* serum response factor; a nuclear, dimeric transcription factor. It forms a complex with **Elk-1** that is constitutively bound to the **serum response element**. Example from human: database code SRF_HUMAN, 508 amino acids (51.54 kDa).
SRIF *abbr. for* somatotropin release-inhibiting factor (i.e. **somatostatin**).
sRNA *or* **S-RNA** *abbr. for* soluble RNA (an early name for **transfer RNA**).
SRP *abbr. for* signal recognition particle.
SR protein any protein belonging to a family of pre-messenger RNA splicing factors possessing highly related primary amino-acid sequences. They share an N-terminal RNA recognition motif and a C-terminal domain that varies in length and consists almost exclusively of alternating serine (S) and arginine (R) residues, from which the proteins are named. Many animal cells possess a series of SR proteins of similar molecular mass: 20, 30, 40, 55, and 70–75 kDa; as yet these have undetermined specificities.
SRS *or* **SRS-A** *abbr. for* slow reacting substance (of anaphylaxis).
S→R variation *see* **smooth–rough variation**.
SSB protein *abbr. for* single-strand binding protein.
SSCP analysis *abbr. for* single-strand conformation polymorphism analysis.
ssDNA *see* **DNA**.
St *symbol for* stokes (a cgs unit of kinematic viscosity).
Sta *symbol for* statine.
stability constant *symbol*: K_s; an equilibrium constant for the reversible formation of a complex chemical compound from two or more simpler entities; the reciprocal of the **dissociation constant**. In some cases, an **apparent stability constant** (*symbol*:

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K'_s), constrained with respect to certain variables (e.g. pH) is determined (for the distinction see **equilibrium constant**). The stability constant is also known as the **association constant** (*symbol*: K_{ass}) in cases where ions associate into a substance, e.g. for the reaction $A^+ + B^- = AB$, the (concentration) stability or association constant is given by:

$$K_s = [AB]/[A^+][B^-] = K_{ass}.$$

stable factor *an alternative name for* factor VII; *see* **blood coagulation**.

stable isotope an **isotope** that is not radioactive.

stachyose *or* **lupeose** the tetrasaccharide, *O*-α-D-galactopyranosyl-(1 → 6)-*O*-α-D-galactopyranosyl-(1 → 6)-*O*-α-D-glucopyranosyl-β-D-fructofuranoside. It is widely distributed, usually associated with **raffinose** (*see* that entry for synthesis) and **sucrose**; it is isolated from *Stachys tuberifera* rhizomes.

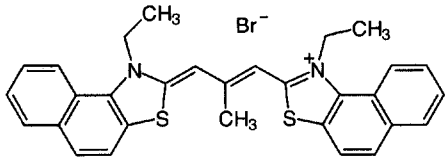
stacking gel *an alternative name for* **spacer gel**.

Staden, R. US molecular biologist; the author of a much used suite of computer programs for sequence analysis of nucleic acids and proteins, available for both **VMS** and **UNIX**.

staggered conformation *see* **conformation**.

stainless steel steel that is resistant to corrosion due to its high content of chromium and, often, nickel. It is highly resistant to all organic acids and weak mineral acids but is slowly attacked by concentrated mineral acids. It does not rust.

Stains-all *a proprietary name for* 1-ethyl-2-[3-(3-ethylnaphtho[1,2-*d*]thiazolin-2-ylidene)-2-methylpropenyl]naphtho[1,2-*d*]thiazolium bromide; a cationic carbocyanine metachromatic dye used as a semiselective stain for locating nucleic acids, proteins, and polysaccharides. RNA stains bluish-purple, DNA blue, protein red, and phosphoprotein blue.



stamp collecting according to Lord Rutherford (1871–1937), one of the two branches of science (the other being physics).

standard *(in analytical chemistry)* **1 primary standard** a chemical that can be obtained in an unvarying state (e.g. of purity and/or stability) and used as an approved example against which other examples of the same chemical can be compared. **2 secondary standard** a chemical that can be used for comparative purposes following calibration against a primary standard. Although its properties are less stringent than a primary standard, its ready availability makes for convenience of use. *See also* **standard atmosphere**, **standard state**, **standard temperature and pressure**.

standard atmosphere an internationally established reference for pressure, defined as 101 325 pascals. The **atmosphere** (def. 3) (*symbol*: atm), equal to 101 325 pascals, was formerly used as a unit of pressure; its use is now discouraged. *See also* **standard temperature and pressure**.

standard curve a plot of any appropriate parameter against known amounts (or concentrations) of detectable substance. Such a curve can be used to determine the amount (or concentration) of the same substance in an unknown solution given a reading for the parameter in the unknown solution.

standard deviation *abbr.*: SD; *symbol*: *s* (for a sample) *or* σ (for a distribution); the common measure of dispersion of a series of observations of *x* that is normally distributed. It is the root-mean-square average of the deviations of the observations from their mean and is in the same units as those of the observations. The standard deviation, s_x, is given by:

$$s_x = \sqrt{\left[\frac{1}{n}\sum_{i=0}^{n}(x-\bar{x})^2\right]}$$

Where $\bar{x}$ is the arithmetic average of deviations of x and n is the number of observations; s_x^2 is called the variance of the sample of observations of x. Some authorities prefer the definition:

$$s_x = \sqrt{\left[\frac{1}{n-1}\sum_{i=0}^{n}(x-\bar{x})^2\right]}$$

so that s_x^2 is then the best estimate of the variance, σ^2, of the population from which the sample of observations of $\bar{x}$ was made. *See also* **degrees of freedom**, **standard error of estimate of the mean**.

standard error of estimate of the mean *or* **standard error of the mean** *abbr.*: SEM; a measure of the reliability of an estimate of the **mean** of a population. It is equal to the **standard deviation**, s_x, of the observations divided by the square root of the number of observations, n; i.e. SEM = $s_x/\sqrt{n}$.

standard free energy *see* **Gibbs energy**.

standardize *or* **standardise** to relate any instrument, vessel, or reaction to an absolute standard. —**standardization** *or* **standardisation** *n*.

standard pressure *symbol*: *p*; an established reference for pressure. Since 1982 the recommended standard pressure for reporting thermodynamic data has been set at 10^5 pascals (1 bar). Before 1982 it was taken to be 101 325 pascals (1 atmosphere).

standard state a set of conditions, established by convention, under which a standard reference is determined or calculated. *See* **chemical potential**, **enthalpy**, **entropy**, **Gibbs energy**, **hydrogen electrode**, **standard pressure**, **standard temperature and pressure**.

standard temperature and pressure *abbr.*: stp *or* s.t.p. *or* STP; the standard conditions for the comparison of properties of gases. Standard temperature is now 298.15 K (formerly 273.15 K, i.e. 0 °C) and **standard pressure** is 10^5 pascals. *Former name*: normal temperature and pressure (*abbr.*: ntp *or* n.t.p. *or* NTP).

Stanley, Wendell Meredith (1904–71), US biochemist; Nobel Laureate in Chemistry (1946) jointly with J. H. Northrop 'for their preparation of enzymes and virus proteins in a pure form' [prize shared with J. B. Sumner].

Staphylococcus a genus of Gram-positive bacteria, commonly associated with wounds and generally causing localized infections. *Staphylococcus aureus* forms yellow or orange pigments and yields plasmids that are useful in recombinant DNA experimentation: *S. aureus* plasmids coding for resistance to various antibiotics can be transfected into *Escherichia coli* or into *Bacillus subtilis* where they are stable, replicate, and express antibiotic resistance. They have provided the basis from which improved vectors have been developed.

starch the most important reserve polysaccharide found in plants. It is a glucan consisting of two components: **amylose**, which is a homopolymer of glucose units linked only by α(1 → 4) bonds; and **amylopectin**, also a glucose homopolymer (branched) that contains α(1 → 6) bonds as well as α(1 → 4) bonds. Starch is synthesized as a temporary storage form of fixed carbon in chloroplasts during active periods of photosynthesis, accumulating as starch grains. The starch is subsequently converted to sucrose and translocated to storage organs, such as seeds and tubers, where it is re-formed. *Compare* **glycogen**.

starch (bacterial glycogen) synthase EC 2.4.1.21; *recommended name*: starch synthase; *systematic name*: ADPglucose:1,4-α-D-glucan 4-α-D-glucosyltransferase; *other name*: ADPglucose–starch glucosyltransferase. An enzyme that catalyses a reaction between ADPglucose and (1,4-α-D-glucosyl)$_n$ to form (1,4-α-D-glucosyl)$_{n+1}$ and ADP. It uses ADPglucose instead of the UDPglucose of **glycogen synthase**. Example from *Escherichia coli*: database code GLGA_ECOLI, 477 amino acids (52.48 kDa).

starch phosphorylase *see* **α-glucan phosphorylase**.

starch synthase EC 2.4.1.11; *recommended name (example)*: glycogen (starch) synthase (the nature of the synthetic product should be included in the name); *systematic name*: UDPglucose:glycogen 4-α-D-glucosyltransferase; *other name*:

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UDPglucose–glycogen glucosyltransferase. An enzyme that catalyses a reaction between UDPglucose and (1,4-α-D-glucosyl)$_n$ to form (1,4-α-D-glucosyl)$_{n+1}$ and UDP. Example (precursor) from maize chloroplasts: database code UGST_MAIZE, 605 amino acids (65.89 kDa). *See also* **glycogen synthase**. *Compare* **starch (bacterial glycogen) synthase**.

starch syrup *an alternative name for* **corn syrup**.

Start an important checkpoint in the G_1 phase of the eukaryotic **cell-division cycle**. Passage through Start commits the cell to enter S phase.

start codon the trinucleotide **codon** AUG that codes for *N*-formylmethionine, the first amino-acid residue in the synthesis of all prokaryotic and mitochondrial proteins.

start kinase a complex of Cdc2 (*see* ***cdc* gene**) and a G_1 **cyclin** that functions as a serine/threonine protein kinase; its activation is necessary for the cell to pass **Start**. The G_1 cyclin that interacts with Cdc2 is thought to be any of several. The identity of the G_1 cyclin modifies the specificity of the complex.

start point the base pair in DNA at which the first nucleotide is incorporated into an RNA transcript. It is most often a purine, and in many cases is the central base of the sequence CAT. It is sited at the downstream end of the **promoter**. *Compare* **start codon**.

start protein any protein that is involved uniquely at the start of the cell cycle. Example, protein Cdc10 from *Schizosaccharomyces pombe*: database code CC10_SCHPO, 767 amino acids (85.42 kDa). This protein (which has a close homologue in *Saccharomyces cerevisiae*) is probably a transcriptional regulator for *cdc10* and also for *cdc2*, which encodes a component of **start kinase**.

starve to deprive of nutrients. In animal experiments a minimum of 24 h deprivation is generally understood. Cultures may be starved of specified single nutrients.

stasis arrest or stagnation of flow.

+stasis *comb. form* denoting lack of movement; cessation of flow. —**+static** *adj.*

STAT *abbr. for* signal transducer and activator of transcription; a family of eukaryotic transcription factors that mediate the response to many cytokines and growth factors. Upon receptor activation, STAT proteins dimerize, translocate to the nucleus, and bind to specific promoter sequences on target genes. Seven different genes have been so far identified in mammals. Example: STA1_HUMAN, 750 amino acids (87.33 kDa).

+stat *comb. form* indicating a device for maintaining a particular property at a constant value, e.g. **cryostat**, **thermostat**. —**+static** *adj.*

stathmin *other names*: phosphoprotein p19; oncoprotein p18; prosolin; an ubiquitous phylogenetically conserved cytoplasmic protein that serves as a phosphorylated intermediate in diverse second-messenger pathways. Stathmin undergoes phosphorylation; both phosphorylation and expression of the protein are regulated throughout development, in response to extracellular signals that control cell proliferation and differentiation. It is a major phosphorylation substrate in neurons. Example (precursor) from *Rattus norvegicus*: database code STHM_RAT, 148 amino acids (17.14 kDa).

+static *see* **+stasis**, **+stat**.

statics *functioning as sing.* the branch of applied mathematics dealing with the interaction of forces in nonmoving systems.

statin **1** a phosphoprotein present specifically in the nuclei of nonproliferating cells. It forms a complex with a 45 kDa serine/threonine protein kinase, and has structural similarity to the **elongation factor** EF-1α. Example from rat: database code STTN_RAT, 463 amino acids (50.28 kDa). **2** *a variant spelling of* **statine**.

+statin *word ending (in hormone nomenclature)* denoting a hypothalamic release-inhibiting factor (or hormone). *Compare* **+liberin**.

statine *or* **statin** *symbol*: Sta; [3*S*,4*S*]-4-amino-3-hydroxy-6-methylheptanoic acid; a novel amino acid contained in positions 3 and 5 of **pepstatin A**.

stationary phase **1** *(in chromatography)* the immobile phase to which the analyte adsorbs or partitions from the mobile phase. **2** *(in fermentation)* the phase of an *in vitro* culture of microorganisms or eukaryotic cells that follows the exponential growth phase and in which there is little or no growth.

statistically significant *see* **significant**.

statistical mechanics the theoretical analysis of molecular properties based on quantum theory.

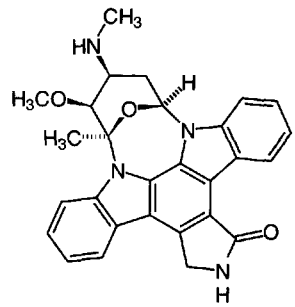
statistical sample a finite selection of items from a population of which the measurement of a variable will give a close approximation to the distribution of that variable in the whole population. *See also* **random sample**, **sample**.

statistics **1** *functioning as sing.* the science of collecting, analysing, interpreting, and presenting quantities of numerical data. **2** *functioning as pl.* a collection of quantitative data. —**statistical** *adj.*

statyl the acyl group derived from **statine**.

Staudinger, Hermann (1881–1965), German chemist; Nobel Laureate in Chemistry (1953) 'for his discoveries in the field of macromolecular chemistry'. Hew was particularly distinguished for his work on polymers such as polystyrene.

staurosporine an antibiotic from *Streptomyces* spp., M_r 466.2, best known as a potent inhibitor of protein kinase C.



Ste *symbol for* the stearoyl group, CH_3 –$[CH_2]_{16}$–CO–.

steady state a condition in which the properties of any part of a system are constant during a process or reaction; i.e. where the rate of formation or increase of a particular quantity is balanced by its rate of removal or decrease.

steady-state fluorescence anisotropy a method in which a sample containing a fluorescent compound is irradiated with plane-polarized light, the emitted fluorescence being analysed to determine its degree of polarization both in the plane of the excitation radiation and in a plane at right angles to this. Only molecules of the fluorescent compound that are aligned in the plane of the incident radiation can absorb radiation and be excited to emit fluorescence. If, in the interval between absorption of the radiation and the emission of fluorescence, the molecule moves out of the plane of polarization of the incident radiation, the emitted radiation will lose polarization (be depolarized) to a degree that depends on the extent to which the molecule had moved. The technique is used to measure the degree to which fluorescent probes are tumbling in a sample. If the probes are held in a relatively rigid position, the extent of depolarization will be small, if tumbling freely it will be high.

steady-state kinetics the analysis of an enzyme reaction in the steady state, i.e. after the pre-steady state and when the intermediates have reached a steady concentration. The duration of the steady state is relatively short, and this state is in any case an approximation since the accumulation of products and the depletion of substrate occur continuously from the start of the reaction. *See* **Michaelis kinetics**.

steapsin *an old term for* **pancreatic lipase**.

stearate **1** *a trivial name for* octadecanoate, CH_3–$[CH_2]_{16}$–COO^-, the anion derived from stearic acid, or octadecanoic acid, a saturated straight-chain higher fatty acid. **2** any

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mixture of free stearic acid and its anion. **3** any salt or ester of stearic acid. *See also* **stearoyl**.

stearin **1** *an old name for* any of the glyceryl esters of stearic acid, especially the triester, **tristearin** (tristearoylglycerol). **2** *a commercial name for* a grade of stearic acid containing other fatty acids, especially palmitic acid.

stearoyl *symbol*: Ste; *numerical symbol* 18:0; *a trivial name for* octadecanoyl, $CH_3–[CH_2]_{16}–CO–$, the acyl group derived from stearic acid (*see* **stearate**). It is one of the major fatty-acid components of plant and animal lipids; tallow and other hard animal fats contain up to 35%. Together with palmitate it represents a high proportion of the saturated fatty-acid content of dietary and other lipids. It is synthesized from palmitoyl-CoA by a microsomal chain-elongation enzyme. It was formerly and sometimes still is (incorrectly) referred to as **stearyl**.

stearoyl-CoA desaturase EC 1.14.99.5; *systematic name*: stearoyl-CoA,hydrogen donor:oxygen oxidoreductase; *other names*: acyl-CoA desaturase; fatty-acid desaturase; Δ^9-desaturase. An enzyme that catalyses a reaction between dioxygen, an electron donor and stearoyl-CoA to form oleoyl-CoA. It is an iron protein with a short half-life, and is the only inducible component of the endoplasmic reticulum fatty acyl-CoA desaturase system. It utilizes electrons from reduced cytochrome b_5. Example from rat: database code ACOD_RAT, 358 amino acids (41.44 kDa).

stearyl **1** *a common name for* octadecyl, $CH_3–[CH_2]_{16}–CH_2–$, the alkyl group derived from octadecane; octadecyl is recommended. **2** *an old trivial name for* octadecanoyl; **stearoyl** now used instead.

steatite *see* **talc**.

steato+ *comb. form* indicating presence or relation to fatty substances.

steatorrhoea the presence of abnormally large amounts of fat in the feces.

steatosis fatty degeneration of tissue.

steel factor *see* **stem cell factor**.

steel factor receptor *see* ***KIT***.

stefin *see* **cystatin**.

Stein, William Howard (1911–80), US protein chemist; Nobel Laureate in Chemistry jointly with S. Moore (1972) 'for their contribution to the understanding of the connection between chemical structure and catalytic activity of the active centre of the ribonuclease molecule' [prize shared with C. B. Anfinsen]. In addition to this he, together with Moore, was responsible for devising the means for automatic analysis of the amino-acid constituents of protein hydrolysates, and free amino acids in body fluids, separated by ion-exchange chromatography.

Stelazine *see* **trifluoperazine**.

stellacyanin a blue copper-containing mucoprotein of low molecular weight obtained from the Japanese lacquer tree, *Rhus vernicifera*. It functions as an electron-transfer protein, accepting electrons from the cytochrome $b_6–f$ complex and donating them to **photosystem** I, and has been much studied for the structure of the copper-binding site.

STEM *abbr. for* scanning transmission electron microscope.

stem cell any member of the various groups of reserve cells whose role is to replace cells that are destroyed during the normal life of the animal, e.g. blood cells, epithelial cells, spermatogonia, and skin cells. Stem cells can divide without limit; after division, the stem cell may remain as a stem cell or proceed to terminal differentiation. Although appearing morphologically unspecialized, the stem cell may be considered as having reached a state of differentiation where the possibilities for further differentiation are very limited.

stem cell factor (*abbr.*: SCF) *or* **mast cell growth factor** *or* **steel factor** a **cytokine** that stimulates the proliferation of mast cells. It is produced by endothelial cells, fibroblasts, bone marrow cells, and Sertoli cells. A homodimer glycoprotein with type I membrane and soluble forms, it is able to augment the proliferation of both myeloid and lymphoid hemopoietic progenitors. It acts as a ligand for the product of the protooncogene c-*kit* (*see* ***KIT***). Example from human precursor: database code SCF_HUMAN, 273 amino acids (30.86 kDa).

stem name any generic name of a category of similar compounds, enzymes, organisms, etc. that is used also as an affix in forming the specific names of individual members of such a category.

steno+ *or (before a vowel)* **sten+** *comb. form* indicating narrowness.

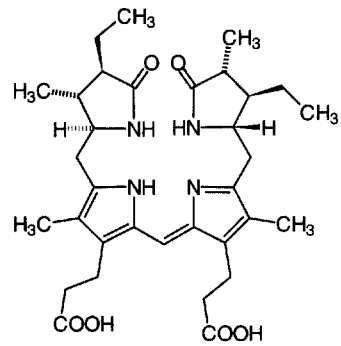
stenohaline describing an organism that is unable to tolerate wide variations in environmental osmotic pressure.

stenothermous describing an organism that is unable to tolerate wide variations in environmental temperature.

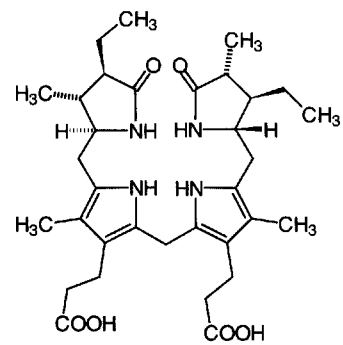
step gradient a discontinuous gradient, formed in a tube by layering solutions of different densities carefully one on the other. In column chromatography the same effect is achieved by pumping buffers of different composition sequentially through the column. *See* **gradient**.

steradian *symbol*: sr; the SI supplementary unit of solid angle. It is equal to the angle subtended at the centre of a sphere by an area of surface equal to the square of the sphere's radius. The surface of a sphere subtends an angle of 4π sr at its centre.

stercobilin *or* **stercobilin IXα** a linear tetrapyrrole formed in heme catabolism with a red brown colour. Structurally it is an oxidation product of **stercobilinogen**, comparable to the **urobilinogen→urobilin** conversion. Metabolically, it is a major product formed from urobilinogen by intestinal bacteria and is the major pigment of feces.



stercobilinogen *an alternative name for* 10,23-dihydrostercobilin; *former name*, stercobilinogen IXα. A product of heme catabolism; it is a linear tetrapyrrole and structurally is a **urobilinogen** molecule in which the double bonds between the methyl and ethyl substituents on the two end rings have been reduced.



sterculic acid *see* **cyclic fatty acid**.

stereo+ *comb. form* denoting solid or three-dimensional.

stereobase unit the smallest set of one, two, or more succes-

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sive **configurational base units** that prescribes repetition in a polymer molecule.

stereochemistry the branch of chemistry dealing with the three-dimensional properties of molecules; the study of the properties of **stereoisomers**. *See* ***cis–trans* isomerism**, ***Re/Si* convention**, **sequence rule**, **stereospecific numbering**.

stereoheterotopic a term describing chemically-like ligands (or faces of double bonds) whose separate replacement with an achiral ligand (or for faces, addition of an achiral reagent) gives rise to two stereoisomers. If the stereoisomeric products are **enantiomers**, the ligands (faces) are enantiotopic; if they are **diastereoisomers**, the ligands (faces) are diastereotopic. for more extensive descriptions, *see* **diastereotopic**, **enantiotopic**.

stereoisomer any of two or more **isomers** that have the same molecular constitution and differ only in the three-dimensional arrangement of their atomic groupings in space. Stereoisomers may be **diastereoisomers** or **enantiomers**. *Compare* **constitutional isomer**. —**stereoisomeric** *adj.*; **stereoisomerism** *n.*

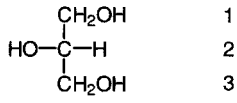
stereology the body of mathematical methods dealing with the interpretation of the structure and dimensions of three-dimensional objects from information contained in two-dimensional representations, such as photomicrographs of tissue sections.

stereoregular polymer a regular polymer composed of molecules having a regular repetition of identical **stereobase units** at all stereoisomeric sites of the main chain.

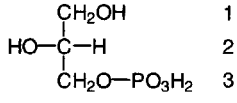
stereoselective polymerization the formation of a polymer from a mixture of stereoisomeric monomer molecules by preferential incorporation of one species into a growing polymer chain.

stereospecific (of an enzymatic or other reaction system) acting on or producing a particular **stereoisomer**; stereochemically specific. —**stereospecificity** *n.*

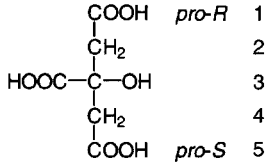
stereospecific numbering a numbering system finding most application for prochiral compounds, *Caabc*, with two chemically-like atoms, or groups of atoms, *a*. It provides identifying numbers for the prochiral *a* groups and, by extension, a numbering system for their chiral derivatives. A stereospecifically numbered compound is designated by the prefix *sn-* to differentiate it from a conventionally numbered compound. Two systems have been described. That of Hirschmann was devised particularly so that the ^{14}C-labelled glycerol giving rise to [3,4-$^{14}C_2$]glucose (in rats) could be termed [1-^{14}C] glycerol and thus be related, biosynthetically and by nomenclature, to [1-^{14}C]lactate. It uses the basic *R/S* system (*see* **sequence rule**) to set up a model, which is viewed away from the group with the lowest sequence priority. If this is *c* in *Caabc*, a counterclockwise ordering is examined for the remaining three groups, *baa*, starting with *b*. The first *a* group to be encountered receives the lower number. The numbering for glycerol is shown in structure 1. By extension, the naturally occurring glycerol phosphate formed by the action of **glycerol kinase** becomes *sn*-glycerol 3-phosphate (structure 2). This structure has also been described as D-glycerol 3-phosphate, L-glycerol 3-phosphate, and L-α-glycerophosphate. The Hirschmann nomenclature has found wide acceptance in the lipid field. The other method, the Hanson and Hirschmann system, expands the *R/S* system in a logical fashion (rather than using the arbitrary counterclockwise ordering described for glycerol). The two chemically-like groups, *a*, of *Caabc* are first given *pro-R* and *pro-S* assignments. Then, following the established '*R* precedes *S* rule', *pro-R* precedes *pro-S*, and the *pro-R* group is assigned the lower number. This system has been applied to citric acid as shown in structure 3. Application of this system to glycerol unfortunately leads to the product of glycerol kinase being *sn*-glycerol 1-phosphate. Although this system has a logical basis in terms of established nomenclature, it seems unlikely that the *sn* system for glycerol and derivatives will be brought into line.



(1) glycerol



(2) *sn*-glycerol-3-phosphate



(3) citric acid

stereospecific polymerization a polymerization in which a **tactic polymer** is formed.

steric relating to effects involving arrangements of atoms in space.

steric hindrance **1** prevention of the free rotation of an atom or group in a molecular entity with respect to a connected one due to the relative sizes and/or spatial disposition of the atoms or groups in question. **2** restriction or prevention of the reaction of a molecular entity with another due to the relative sizes and/or spatial disposition of atoms or groups in either or both of the reactants.

sterile **1** (of inanimate objects) free from microbiological or other life forms. **2** (of a living organism) incapable of sexual reproduction.

sterilize *or* **sterilise** **1** to treat in such a way as to kill undesired microorganisms without damaging the material under treatment. *Compare* **disinfection**. **2** to render incapable of sexual reproduction. —**sterilization** *or* **sterilisation** *n.*

Stern–Volmer equation an expression relating **fluorescence quenching** to the concentration of the quenching substance, *c*, and the fluorescence lifetime, τ. It is: $F_o/F = 1 + kc\tau$, where F_o is the fluorescence intensity when no quencher is present, F is the fluorescence intensity in the presence of quencher, and k is a constant that depends on the system; the concentration of the absorbing molecule must be the same in both quenched and unquenched systems. The **Stern–Volmer plot** is a plot of F_o/F against concentration of quenching substance, from the slope of which, if the fluorescence lifetime is known, the quenching constant can be obtained. [After Otto Stern (1888–1969) and M. Volmer].

steroid any of a large group of substances that have in common a ring system based on 1,2-cyclopentanoperhydrophenanthrene. The group includes such natural products as **bile acids**, **corticosteroids**, **sex hormones**, **sterols**, and various plant steroids. *See also* **vitamin D**.

steroid diabetes a condition involving decreased glucose tolerance, fasting hyperglycemia, and glucosuria, found in patients exposed to excessive quantities of **glucocorticoids**. It may thus accompany **Cushing's syndrome**.

steroid-hormone receptor any member of a family of intracellular receptors that bind steroid hormones and mediate their effects; the family also includes receptors for thyroid

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hormones, retinoids, and vitamin D. After binding steroid that has entered the cell, the steroid–receptor complex is translocated to the nucleus and binds to a specific DNA sequence, a **response element**. The receptors are composed of three domains: a modulating N-terminal domain, a DNA-binding domain, and a C-terminal steroid-binding domain. Their zinc fingers are characteristic (four motifs). Examples (human), steroid-hormone receptor ERR1: database code ERR1_HUMAN, 521 amino acids (55.68 kDa); estrogen receptor: database code ESTR_HUMAN, 595 amino acids (66.18 kDa).

steroid Δ-isomerase EC 5.3.3.1; *systematic name*: 3-oxosteroid Δ^5–Δ^4-isomerase; *other name*: Δ^5–Δ^4-ketosteroid isomerase. An enzyme (dimer) involved in microbial transformation of steroids; it catalyses the reaction:

$$\text{3-oxo-}\Delta^5\text{-steroid} = \text{3-oxo-}\Delta^4\text{-steroid}.$$

Example from *Comamonas testosteroni* (*Pseudomonas testosteroni*): database code SDIS_COMTE, 125 amino acids (13.38 kDa).

steroid 21-monooxygenase EC 1.14.99.10; *other names*: steroid 21-hydroxylase; cytochrome P450 21A1; an enzyme that catalyses a reaction between dioxygen, an electron donor, and a steroid to form a 21-hydroxysteroid. It is a heme–thiolate protein. A deficiency underlies congenital adrenal hyperplasia: there is a failure to synthesize cortisol, and this results in overproduction of **corticotropin**, as well as of 17-hydroxyprogesterone and androstenedione. Example from human: database code CPS1_HUMAN, 494 amino acids (55.82 kDa).

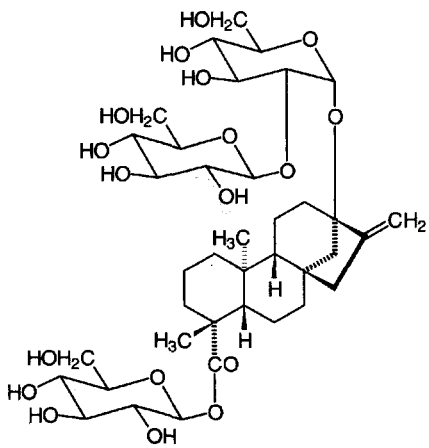
steroidogenesis the biosynthesis of steroids, but often referring to the genesis of other steroids from cholesterol.

sterol any of a group of **steroids** characterized by the presence of one or more hydroxyl groups and a hydrocarbon side-chain in the molecule.

sterol O-acyltransferase EC 2.3.1.26; *other names*: cholesterol acyltransferase; sterol-ester synthase; an intracellular enzyme that catalyses the formation of cholesterol ester from acyl-CoA and cholesterol. It is involved in the storage of cholesterol esters in phagocytic cells, a process that plays a part in producing lipid-laden cells in arterial walls. Example from human: database code ACAT_HUMAN, 550 amino acids (64.77 kDa).

steryl-sulfatase EC 3.1.6.2; *other names*: steroid sulfatase (sulfatase); steryl-sulfate sulfohydrolase; arylsulfatase C; an enzyme that catalyses the hydrolysis of 3-β-hydroxyandrost-5-en-17-one 3-sulfate to 3-β-hydroxyandrost-5-en-17-one and sulfate. Example (precursor) from human: database code STS_HUMAN, 583 amino acids (65.42 kDa).

stevioside 13-[(2-*O*-β-D-glucopyranosyl-α-D-glucopyranosyl)oxy]kaur-16-en-18-oic acid β-D-glucopyranosyl ester; a glycoside extracted from the leaves of *Stevia rebaudiana* (yerba dulce). It is used as a sweetening agent, being about 300 times as sweet as sucrose.

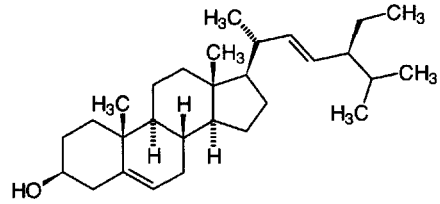


STH *abbr. for* somatotropic hormone; *see* **somatotropin**.

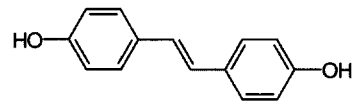
STI *abbr. for* soybean trypsin inhibitor.

sticky end *see* **cohesive end**.

stigmasterol 3β-hydroxy-24-ethyl-$\Delta^{5,22}$-cholestadiene; a **phytosterol** structurally related to β-sitosterol (*see* **sitosterol**) and found in plant oils.



stilbestrol *or (esp. Brit.)* **stilboestrol** 4,4′-dihydroxystilbene; a synthetic nonsteroid compound, first prepared in 1938, that proved to be the mother substance of a range of compounds with estrogenic activity, of which α,β-diethylstilbene (*see* **diethylstilbestrol**) is the most active. Stilbestrol was formerly used as a growth promoter in farm animals but is now banned in most countries. However, it is still sometimes used to treat hormonal disorders in small animals. It was formerly used to treat prostatic cancer but there is some evidence for its carcinogenicity.



trans-stilbestrol

still an apparatus for the distillation of liquids, including the preparation of distilled water. It consists of a heated vessel, a condenser, and a receiver. A continuous apparatus incorporates an automatic feed for the liquid in question, a heating element, and a thermoregulator.

stimulate *(in physiology)* to provide a **stimulus** to any tissue or cell leading to its excitation or to initiation of a sequence of events with some defined endpoint, involving an electrical event, activation of a metabolic pathway, or initiation of cell division or growth. —**stimulation** *n.*; **stimulative** *adj.*

stimulus *(in physiology)* any event or phenomenon, such as radiation, electrical potential, or addition of molecules that leads to excitation of a tissue or cell.

stimulus–response coupling a molecular mechanism, often involving **signal transduction**, that transmits a stimulus from the exterior of a cell's plasma membrane, in many cases through **second messenger** pathways, to effector systems that bring about a response. For example, in **stimulus–secretion coupling** the effector system brings about a secretion event such as degranulation of mast cells or release of hormone (e.g. insulin) from storage granules to the cell exterior.

stimulus–secretion coupling *see* **stimulus–response coupling**.

stochastic arrived at by skilful conjecture; e.g. a stochastic model, a stochastic process.

stock solution a solution of a reagent, at a stable or convenient concentration, from which appropriate dilutions can be made at the time of use.

Stock system *(in inorganic nomenclature)* a system of designating the **oxidation number** of an element by placing a Roman numeral in parentheses immediately following the name of the element or, where symbols are used, in superscript to the right of the symbol; e.g. manganese(IV) oxide, $Mn^{IV}O_2$.

stoichiometry *or (rarely)* **stoicheiometry** the quantitative relationship of the reactants and products of a chemical reaction

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in the proportions that they appear in the chemical equation describing the reaction. —**stoichiometric** *or* **stoicheiometric** *adj.*

stokes *symbol*: St; the cgs unit of **kinematic viscosity**; its use is now discouraged. In SI units, kinematic viscosity is measured in square metres per second; 1 St = 10^{-4} m^2 s^{-1}. [After (Sir) George Gabriel Stokes (1819–1903), British mathematician.]

Stokes' law of fluorescence a law stating that the wavelength of the emitted fluorescent light, λ_{em}, is greater than that of the light exciting the fluorescence, λ_{ex}. This relationship is true for most fluorescent materials; those for which it does not hold are termed **anti-Stokes**.

Stokes' law of viscosity a law stating that the frictional coefficient, f, of a spherical particle of radius r, moving through a liquid of viscosity η, is given by $f = 6\pi\eta r$.

Stokes' loss the loss of excitation energy available for fluorescence due to collision of molecules in the first excited state, S_1, with their neighbours, which results in a lower vibration level of S_1.

Stokes' shift the difference in wavelength between the excitation and emission maxima for a particular fluorescent substance. In quantitative form, Stokes' shift is $10^7(1/\lambda_{ex} - 1/\lambda_{em})$, where λ_{ex} and λ_{em} are the corrected maximum wavelengths for excitation and emission expressed in nanometres.

stoma (*pl.* **stomata**) any of the pores occurring in the epidermis of plants, particularly in leaves, through which gaseous exchange takes place.

stop codon any of the trinucleotide **codons**, UGA, UAG, and UAA, that signal the termination of translation of a messenger RNA molecule and the release of the nascent polypeptide chain. *See also* **termination codon**.

stopped-flow technique a method in which two solutions are caused to flow into a mixing chamber and then into an observation chamber, after which the flow is caused to stop abruptly and the time course of the chemical reaction can be followed, usually spectroscopically, as the mixture in the observation chamber ages. Critical features include the quality of mixing, the speed with which the mixed solution fills the observation volume, and the geometry of the observation volume in relation to the sensitivity of observation. *See also* **rapid-reaction kinetics**.

STOP protein *abbr. for* stable tubule only polypeptide; a protein that blocks the endwise dissociation of microtubules.

stop-transfer protein *see* **signal peptide**.

storage granule any small **organelle**, bounded by a membrane having a single lipid bilayer, that contains stored material. For example, mast-cell storage granules contain histamine, while those of pancreatic B cells contain insulin; in both cases the stored material is destined for secretion. This involves a stimulus applied to the cell that causes fusion of the granule membrane with the plasma membrane, followed by release of the granule contents by **exocytosis**.

storage polysaccharide any polysaccharide that serves as a form of stored energy in living organisms. Storage polysaccharides include starch, phytoglycogen (e.g. in maize), and fructosans (e.g. inulin) in plants, and glycogen in animals.

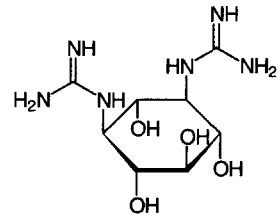
stp *or* **s.t.p.** *or* **STP** *abbr. for* standard temperature and pressure.

straight-chain describing any chain of carbon atoms in which none of the carbon atoms is directly bonded to more than two other carbon atoms.

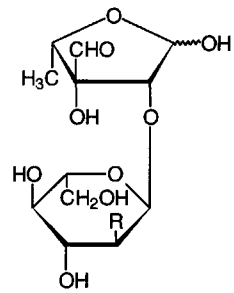
strain **1** a group of related individuals having certain characters that distinguish the members from other such groups within the same species or variety; a race. **2** a line of organisms descended or derived from a particular ancestral individual. **3** *(in physics)* the temporary or permanent deformation of a body resulting from an applied stress.

streptavidin a tetrameric biotin-binding protein (subunit M_r 14 500) produced by *Streptomyces avidinii*, capable of binding up to four molecules of **biotin** per molecule. It is useful in techniques such as enzyme-linked immunosorbent assay (ELISA), radioimmunoassay, immunocytochemistry, and protein blotting. It is also used with DNA probes as a detection reagent, where biotin can be incorporated into the molecule under study; streptavidin can then be used to bind to the biotin. The streptavidin may be labelled with **FITC**, gold, peroxidase, or another agent directly as a detection reagent. Alternatively, a biotin-labelled detection system (such as alkaline phosphatase) can be bound to streptavidin through another of its biotin-binding sites. Streptavidin has the advantage over **avidin** (also used in such techniques) of having a near-neutral isoelectric point (7.25–7.45); consequently its use results in less nonspecific binding. *See also* **biotinylation**.

streptidine 1,3-diguanido-2,4,5,6-cyclohexanetetrol; the non-carbohydrate component of **streptomycin**.



streptobiosamine 5-deoxy-2-*O*-[2-deoxy-2-(methylamino)-α-L-glucopyranosyl]-3-*C*-formyl-L-lyxose; a disaccharide component of **streptomycin**, containing **streptose** and *N*-methylglucosamine.



R = $NHCH_3$

Streptococcus a genus of Gram-positive, facultatively or obligately anaerobic cocci or coccoid bacteria, of biochemical significance for their production of **streptokinase**, **streptolysin**, and **streptodornase**.

streptodornase any of the extracellular deoxyribonucleases produced by streptococci. At least four such serologically distinct nucleases are known. Some or all have the characteristics of **deoxyribonuclease I** (EC 3.1.21.1), bringing about endonucleolytic cleavage of DNA to 5′-phosphodinucleotide and 5′-phosphooligonucleotide end-products. [From streptococcal deoxyribonuclease.]

streptokinase any of a number of extracellular proteins produced by certain streptococci; they exhibit no enzymic activity, despite the name. In human blood streptokinase forms a tight 1:1 complex with **plasminogen** that catalyses the activation of plasminogen to plasmin, and this in turn lyses fibrin clots. It has been used therapeutically after heart attacks and strokes. It is assumed that streptokinase assists the invasiveness of pathogenic streptococci. Example, streptokinase A precursor from *Streptococcus pyogenes*: database code STRP_STRPY, 440 amino acids (49.84 kDa); residues 1–26 are the signal, 27–440 the protein.

streptolydigin an antibiotic, derived from *Streptomyces lydicus*, that possesses potent antibacterial action, particularly against anaerobes and some Gram-positive aerobes. This is probably due to its inhibitory activity against bacterial **RNA**

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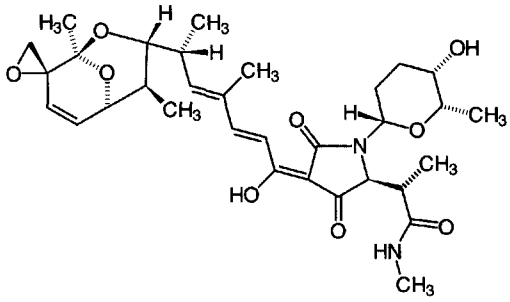
polymerase; it reduces the rate of transcription, slowing the rate of phosphodiester bond formation without affecting the fidelity of transcription. This contrasts with **rifampicin**, which inhibits initiation. *Compare* **rifamycin**.

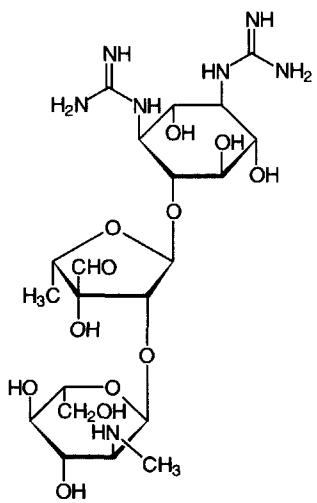


streptolysin either of two dissimilar **hemolysins** produced by certain streptococci (particularly of group A). **Streptolysin-O** (oxygen-sensitive) is produced by culture in serum-free medium. Its hemolytic activity is destroyed by oxygen (but restored by certain mild reducing agents, e.g. 2-mercaptoethanol) and inhibited by free cholesterol. It is immunogenic, the level of circulating antibody (**antistreptolysin-O**, ASO) being useful clinically in the diagnosis of streptococcal infections. Hemolysis by streptolysin-O is not complement-dependent. Streptolysin-O can also lyse lysosomes. Biochemically and serologically it resembles O-toxin of *Clostridium perfringens*. It can be used as an agent to permeabilize cells. **Streptolysin-S** (serum-dependent) is oxygen-insensitive and its production is promoted by serum proteins. Its hemolytic activity is inhibited by certain phosphatides, e.g. phosphatidyl ethanolamine, at low concentration. It is nonimmunogenic, and is also toxic to leukocytes.

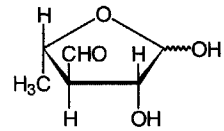
Streptomyces a genus of filamentous, spore-forming, Gram-positive bacteria that are largely responsible for the 'earthy' smell of soil but are chiefly remarkable for the diversity of secondary metabolites that they produce, including clinically useful antibiotics, e.g. **streptomycin**. They are amenable to genetic manipulation with many plasmid and phage vectors; this provides a unique opportunity for overexpression and for the design and synthesis of novel and 'hybrid' antibiotics. *See also* **streptomycete**.

streptomycete strictly, any member of the bacterial genus ***Streptomyces***. However, the term may sometimes be extended to include certain related types, including *Streptoverticillum* spp.

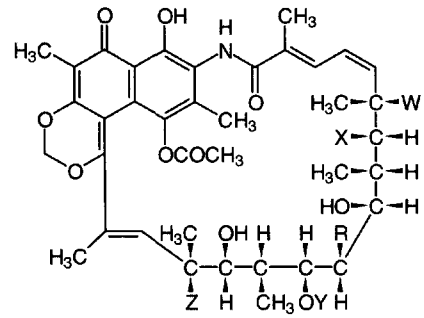
streptomycin an **aminoglycoside antibiotic** produced by the soil bacterium *Streptomyces griseus*, having a relatively broad spectrum of activity against bacteria; it is particularly active against mycobacteria (especially against *Mycobacterium tuberculosis*), enterobacteria, and staphylococci. It acts at the 30S ribosomal subunit and distorts the A site (**aminoacyl site**), thereby causing miscoding or prevention of binding of aminoacyl-tRNA. The components of streptomycin are **streptidine**, **streptose**, and *N*-methyl-L-glucosamine.



streptose L-streptose; 5-deoxy-3-*C*-formyl-L-lyxose; a component of **streptomycin** and **streptobiosamine**.

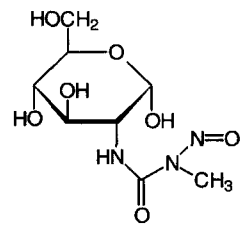


streptovaricin any one of a group of **ansamycin** antibiotics obtained from *Streptomyces spectabilis*. *Compare* **rifamycin**.



Streptovaricin	W	X	Y	Z	R
A	OH	OH	Ac	OH	$COOCH_3$
B	H	OH	Ac	OH	$COOCH_3$
C	H	OH	H	OH	$COOCH_3$
D	H	OH	H	H	$COOCH_3$
E	H	O=	H	OH	$COOCH_3$
G	OH	OH	H	OH	$COOCH_3$
J	H	OAc	H	OH	$COOCH_3$
K	OH	OAc	H	OH	$COOCH_3$

streptozocin 2-deoxy-2-(3-methyl-3-nitrosoureido)-D-glucopyranose; a broad-spectrum antibiotic, antineoplastic, and diabetogenic substance isolated from *Streptomyces achromogenes*. It has a rapid and specific cytotoxic effect on the B cells in pancreatic islets, and is used to induce experimental diabetes in animals and for chemotherapy of insulinoma or other islet-cell neoplasms in humans. It acts as a methylating agent for DNA.



α-D-streptozocin

striated muscle muscle in which the **thick filaments** and **thin fila-**

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ments are arranged in microscopically visible bands producing a striped appearance. Such an arrangement is typical of skeletal muscle and cardiac muscle. *Compare* **smooth muscle**. *See also* **sarcomere**.

strict aerobe *see* **aerobe**.

strict anaerobe *see* **anaerobe**.

stringency *(in molecular biology)* the rigour with which the ability of complementary DNA sequences to recognize each other (and thus to hybridize) is tested. As temperature is increased it becomes less likely that more distantly related sequences will hybridize; hence, high stringency is associated with high temperature.

stringent very rigorous. *See also* **stringency**, **stringent control**, **stringent plasmid**, **stringent response**.

stringent control a mechanism of control of plasmid replication whereby the plasmid is replicated only once for each time the chromosome is replicated, thus regulating the plasmid copy number.

stringent factor a protein associated with ribosomes, and encoded by the gene ***relA***, that is associated with the **stringent response**. The stringent factor is associated with enzyme activity that donates a pyrophosphate group to 3′ of either 5′-GTP or GDP for the production of pppGpp and ppGpp, which probably act as allosteric modulators mediating the stringent response. *See also* **relaxed mutant**, ***spoT***.

stringent plasmid a plasmid that has a limited number of copies per cell.

stringent response a response by bacteria to poor growth conditions (e.g. lack of amino acids) in which the cell shuts down protein synthesis and other metabolic activity. *See also* **relaxed mutant**, **stringent factor**.

strip **1** to remove adherent, admixed, or combined substances or material from a fundamental, underlying, or required substance or structure. **2** *(in molecular biology)* **a** to remove polysomes from rough endoplasmic reticulum *in vitro* to produce **stripped membranes** (*see* **degranulation** (def. 2)). **b** to remove ribosomal proteins from a ribosome to produce a **core particle**. **c** to remove the amino acid from an aminoacyl-transfer RNA molecule to produce **stripped transfer RNA**. **d** to remove hybridized **probe** (def. 3) from a **transfer membrane** prior to reprobing. **3** *(in biochemistry)* to remove endogenous 2,3-bisphosphoglycerate from a hemoglobin solution to produce **stripped hemoglobin**. **4** to remove liquid components from a gaseous mixture.

stripped hemoglobin a hemoglobin solution from which endogenous 2,3-bisphosphoglycerate has been removed, e.g. by gel filtration or dialysis at high NaCl concentrations.

stripped membrane rough endoplasmic reticulum from which polysomes have been removed *in vitro*. This technique has been applied mainly to membranes from dog pancreas, which lack ribonuclease; the ribosomes are removed by treatment with EDTA.

stripped transfer RNA a molecule of aminoacyl-transfer RNA from which the amino acid has been hydrolytically removed.

stroma (*pl.* **stromata**) **1** fibrous connective tissue or other intercellular material that forms the structural framework of an organ, as opposed to the functional tissue (parenchyma). **2** the spongy framework of protein strands within a red blood cell in which the hemoglobin is packed. **3** *(in botany)* the space enclosed by the double membrane of a **chloroplast** but excluding the thylakoid space. It contains DNA, ribosomes, and some temporary products of photosynthesis. **4** *(in mycology)* a mass of interwoven hyphae in which fruiting bodies (perithecia) develop. —**stromal** *adj.*

stromelysin EC 3.4.24.17; *other names*: matrix metalloproteinase-3 (*abbr.*: MMP-3); transin-1; an enzyme that catalyses the degradation of fibronectin, laminin, and some (but not all) gelatins and collagens. Zn^{2+} and Ca^{2+} are cofactors. It is a glycoprotein of the extracellular matrix. Example, stromelysin 1 precursor from human: database code COG3_HUMAN, 477 amino acids (53.92 kDa).

strong acid an **acid** that remains ionized at all except the lowest pH values, i.e. one that has a large **acid dissociation constant**.

strong base a **base** that remains ionized at all except the highest pH values, i.e. one that has a large **basic dissociation constant**.

strophanthin a highly toxic glycoside mixture produced by *Strophanthus kombe*, with actions similar to those of **digoxin** and **ouabain**.

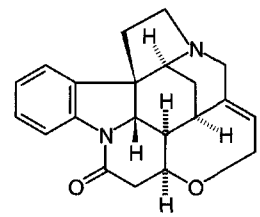
structural gene any gene that carries the genetic information determining the structure, and therefore the specificity of function, of a protein. One or more structural genes may be contained in an **operon**. *Compare* **regulator gene**.

structural polysaccharide any of several components of a plant cell wall that perform a structural function. They can be divided into three solubility classes: **pectins**, extractable with dilute acid; **hemicelluloses**, extractable with aqueous alkali; and **microfibrillar polysaccharides**.

structure factor a parameter describing the scattering of electromagnetic radiation (e.g. X-rays) by an electron. It is the ratio of the radiation scattered by any real sample to that scattered by a single electron at the origin.

Strutt, John William, Lord Rayleigh (3rd Baron Rayleigh) (1842–1919), British mathematician and physicist noted *inter alia* for his contributions to the theory of sound, for his investigations of physical optics, e.g. **Rayleigh scattering**, and for his discovery (with W. Ramsay) of argon; Nobel Laureate in Physics (1904) 'for his investigations of the densities of the most important gases and for his discovery of argon in connection with these studies'.

strychnine a bitter alkaloid obtained from seeds of the Indian tree *Strychnos nux-vomica*. It is highly toxic, and is sometimes used to poison moles, rodents, and other vermin. Its lethal convulsant action is a result of antagonism of the inhibitory transmitter, glycine, in the spinal cord (*see* **glycine receptor**). *See also* **brucine**.



STS *abbr. for* sequence-tagged site.

Stuart factor *or* **Stuart–Prower factor** *an alternative name for* factor X; *see* **blood coagulation**. [After a Mr Stuart, in whom the deficiency was first described.]

Student's *t* test a statistical test, based on a distribution due to William Sealy Gosset (1876–1937) writing in 1908 under the pseudonym 'Student', that can be applied to small samples of data, x. In this distribution t depends only on the sample size, N, and not on the variance of the population; as N increases, the distribution curve of t approaches a normal distribution curve more closely.

STX *abbr. for* saxitoxin.

sU *symbol for* a residue of the ribonucleoside thiouridine (when the position of the thiol group in its thiouracil moiety is unspecified or unknown; alternative to S or Srd).

s^{2}U *symbol for* a residue of the ribonucleoside 2-thiouridine (alternative to ^{2}S).

s^{4}U *symbol for* a residue of the ribonucleoside 4-thiouridine (alternative to ^{4}S).

sub *jargon term for* **subculture** (def. 1).

sub+ *prefix* **1** beneath, under, at the bottom (of). **2** immediately below in order, rank, or status; secondary. **3** less than, partial(ly), imperfect(ly). **4** in place of. **5** denoting a subordinate part or subdivision of a whole. **6** *(in chemical nomenclature)* designating a compound that contains less than the usual pro-

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portion of a specified element; e.g. carbon suboxide, C_2O_3. *Compare* **infra+**, **super+**.

subcellular describing organelles, functional units, or other components that are found within cells or derived from cells.

subcellular organelle a pleonasm that is commonly used to describe **organelles** (which by definition are subcellular).

subclone to clone into a new vector a subfragment of part of a larger cloned DNA, after excising the required fragment using restriction endonucleases.

subculture **1** to prepare a fresh culture from a small sample of an existing culture. **2** a culture prepared in such a way.

subcutaneous *abbr.*: s.c.; below the skin.

suberin the polymeric substance that covers the epidermal cell layer in the underground parts of plants (e.g. roots and tubers). It is a polyester containing ω-hydroxy fatty acids and aromatic fatty acids, e.g. **ferulic acid**.

sublime to vaporize from the solid without passing through a liquid phase. —**sublimation** *n.*

submaxillaris protease an endopeptidase isolated from the submaxillary gland of mice. It acts specifically at Arg-|-Xaa bonds.

submaxillary relating to the region beneath the upper jaw (maxilla).

submaximal below the maximal.

submitochondrial particle any particle derived by disruption of mitochondria. *See* **H^+-transporting ATPase, complex I, II, III, IV**.

submolecular describing any chemical or chemical component that exists or functions at a lower level of complexity than that of intact individual molecules. The term may be used in reference to electrons, ions, free radicals, or other molecular fragments. *Compare* **supramolecular**.

subnatant **1** lying under. **2** a liquid lying under a **supernatant** or under solid material. *Compare* **infranatant**.

suboptimal below or failing to reach the optimal condition.

subsite a site, e.g. on a protein, that has a specific function within the overall function of a larger site.

substance K *see* **neurokinin A**.

substance K receptor *or* **neurokinin A receptor** *or* **NK-2 receptor** a membrane protein that binds substance K and mediates its intracellular effects. It is a G-protein-coupled, seven-transmembrane-domain protein that activates the **phosphatidylinositol cycle**. Example from *Bos taurus*: database code NK2R_BOVIN, 384 amino acids (43.07 kDa).

substance P *abbr.*: SP; an 11-residue amide,

H-Arg-Pro-Lys-Pro-Gln-Gln-Phe-Phe-Gly-Leu-Met-NH_2,

found in most tissues of the mammalian body but at highest concentrations in nervous tissue (both central and peripheral) and in gut tissues. It also occurs in the central nervous system of many other vertebrtates. Derived from **protachykinin β precursor**, it is a **tachykinin**; its main pharmacological actions are to cause hypotension and vasodilatation, and to stimulate contraction of the intestine and secretion of saliva. However, its physiological function remains to be fully determined. *See also* **tachykinin receptor**.

substituent group *or* **substituent** *(in organic-chemical nomenclature)* any atom or **group** (def. 1) that has replaced or can be considered to have replaced (i.e. been substituted for) a hydrogen atom in a parent molecular entity, which may be either real or hypothetical; in the special cases of bivalent or tervalent groups there are corresponding replacements of two or three hydrogen atoms.

substituted mechanism a mechanism of an enzyme reaction in which the first substrate reacts with the original enzyme to produce a modified enzyme and one product. The modified enzyme then reacts with the second substrate to produce the second product and regenerate the original enzyme, e.g.

$$E + S_1 \rightleftharpoons E^* + P_1,$$

then

$$E^* + S_2 \rightleftharpoons E + P_2,$$

where E is the enzyme, E* the modified enzyme, S_1 and S_2 the substrates, and P_1 and P_2 the products.

substitution reaction the replacement of a substituent (normally hydrogen), usually at a carbon atom, by any other group.

substrate **1** a substance that is acted upon, especially by an enzyme; a molecule or structure whose transformation is catalysed by an enzyme. **2** *or* **substratum a** the base upon which an organism grows or lives, e.g. soil or rock. **b** the material upon which a microorganism grows or is placed to grow.

substrate activation the increase of an enzyme's activity by its substrate by an **allosteric** mechanism. *Compare* **substrate inhibition**.

substrate cycle interconversion of reactant and product by two enzymes, one of which (A) catalyses the reaction in one direction while the second enzyme (B) catalyses the reaction in the opposite direction, e.g.

$$\text{fructose 6-phosphate} \underset{B}{\overset{A}{\rightleftharpoons}} \text{fructose 1,6-bisphosphate}.$$

As **flux** (def. 3) (i.e. the rate of reaction catalysed by A minus rate of reaction catalysed by B) through a system varies, the rate of each enzyme reaction may vary independently with concomitant changes in cycling rate. The existence of a substrate cycle increases sensitivity of control, since even if rates of forward and reverse reaction are high, changes in one or both may make relatively larger changes to flux; e.g. if rate of A = 9 and rate of B = 8, then flux = 1; if rate of A doubles to 18 and rate of B remains 8, then flux = 10 (i.e. increases tenfold).

substrate dissociation constant *or (formerly)* **substrate constant** *symbol* K_s; the parameter of an enzymatic reaction that is the equilibrium (dissociation) constant for the reaction ES = E + S; i.e. K_s = [E][S]/[ES].

substrate inhibition the inhibition of an enzyme's activity by its substrate by an **allosteric** mechanism. *Compare* **substrate activation**.

substrate-level phosphorylation the formation of ATP (or GTP) in a coupled reaction that is not linked to an electron transport system, e.g. coupled to the deacylation of succinyl coenzyme A or the conversion of 3-phosphoglyceroyl phosphate to 3-phosphoglycerate.

substrate-site hypothesis a hypothesis for the control of insulin release from pancreatic islet B cells by glucose. It postulates that the glucoreceptor is either a carrier transporting glucose into the cell or an enzyme phosphorylating glucose, and the signal for insulin release is a metabolite in the pathway of metabolism of glucose in the B cell. *Compare* **regulator-site hypothesis**.

substratum (*pl.* **substrata**) **1** any layer (stratum) or structure that lies beneath another, or that forms a base or underlying support for something else. **2** *an alternative term for* **substrate** (def. 2).

subtiligase one of several engineered derivatives of **subtilisin** that efficiently ligate peptides. The two mutations converting the peptidase, subtilisin, to a ligase involve Ser^{221} to Cys and Pro^{225} to Ala.

subtilin *or* **subtilin C** an antibiotic produced by *Bacillus subtilis* and active against Gram-positive bacteria, *Neisseria* spp. (*N. catarrhalis*, *N. gonorrhoeae*), and some pathogenic fungi.

subtilisin EC 3.4.21.62; a bacterial endopeptidase enzyme isolated from *Bacillus subtilis* and other *Bacillus* spp. (e.g. commercially from *B. licheniformis*). It is a **serine endopeptidase** that catalyses the hydrolysis of proteins with broad specificity for peptide bonds, with preference for a large uncharged residue at P1 (*see* **peptidase P-sites**) and low activity for glutamyl residues; it hydrolyses peptide amides. Example from *B. subtilis*: database code NRL_1SBC, 274 amino acids (27.26 kDa); 3-D structure is known; the enzyme has similar active-site geometry to the trypsin family but otherwise no homology. *See also* **Nagarse proteinase**.

subtrahend *(in mathematics)* the number to be subtracted from another number (the minuend).

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subunit any polypeptide component within a protein or other distinct biochemical entity, whether identical to or different from any other components, that is separable from such other components without rupture of covalent bonds. The term is sometimes used in a more restricted sense as referring to any chemically or physically identifiable submolecular entity within a protein, whether identical to, or different from, other components.

subunit-exchange chromatography a form of chromatography in which protein subunits are immobilized on a solid matrix and allowed to interact with protein subunits in solution. Quantification of subunit exchange between the matrix and solution may be used in analysing the association–dissociation properties of the protein system. The method also provides a powerful, specific purification method.

Suc– *symbol for* **succinyl** (def. 1).

–Suc– *or* **Suc<** *symbol for* **succinyl** (def. 2).

succinamic acid *a trivial name for* 3-carbamoylpropanoic acid, the monoamide of succinic acid.

succinamide *a trivial name for* butanediamide, the diamide of succinic acid.

succinate **1** *a trivial name for* butanedioate; ethanedicarboxylate; the dianion of succinic acid. It is an important intermediate in metabolism and a component of the **tricarboxylic-acid cycle**. **2** any mixture of free succinic acid and its mono- and dianions. **3** any salt or ester of succinic acid.

succinate–CoA ligase (GDP-forming) EC 6.2.1.4; *other name*: succinyl-CoA synthetase (GDP-forming); an enzyme of the tricarboxylic-acid cycle that catalyses the formation of succinyl-CoA from GTP, succinate, and CoA with release of GDP and orthophosphate. Examples: α-chain precursor from rat: database code SUCA_RAT, 333 amino acids (34.99 kDa); β chain (from pig): database code A44529, 417 amino acids (45.10 kDa).

succinate dehydrogenase EC 1.3.99.1; *systematic name*: succinate:(acceptor) oxidoreductase; *other names*: fumarate reductase/dehydrogenase; fumaric hydrogenase. A bacterial enzyme, or a degraded entity from **succinate dehydrogenase (ubiquinone)**, a major component of mitochondrial complex II (*see* **respiratory complex**). It catalyses the oxidation of succinate by an acceptor to form fumarate and a reduced acceptor; it does not react with ubiquinone. It is a flavoprotein (FAD) and plays an important role during anaerobic growth. Example from *Escherichia coli*; there are four subunits: (1) cytochrome b_{556}; (2) an iron–sulfur protein: database code DHSB_ECOLI, 238 amino acids (26.74 kDa); (3) a flavoprotein related to succinate dehydrogenase (ubiquinone): database code DHSA_ECOLI, 588 amino acids (64.33 kDa); and (4) a hydrophobic anchor protein.

succinate dehydrogenase (ubiquinone) EC 1.3.5.1; *systematic name*: succinate:ubiquinone oxidoreductase; *other name*: succinic dehydrogenase. An enzyme that catalyses the oxidation of succinate by ubiquinone to form fumarate and ubiquinol. It is an iron–sulfur flavoprotein (FAD), containing at least four different subunits: a flavoprotein, an iron–sulfur protein, and two hydrophobic anchor proteins. It is located in the mitochondrial inner membrane, where it is a major component of complex II (*see* **complex I**, **II**, **III**, **IV**) of the **respiratory chain**. Example, FAD, subunit (precursor) from bovine: database code DHSA_BOVIN, 664 amino acids (73.63 kDa). Two other examples (subunits, precursors, from yeast); flavoprotein subunit: database code DHSA_YEAST 640 amino acids (70.15 kDa); iron-sulfur protein subunit: database code DHSB_YEAST 266 amino acids (30.20 kDa).

succinate-semialdehyde dehydrogenase EC 1.2.1.24; an enzyme that catalyses the reaction:

$$\text{succinate semialdehyde} + NAD^+ + H_2O = \text{succinate} + NADH.$$

Succinate semialdehyde can undergo transamination to form γ-aminobutyric acid. However, the transaminase primarily functions to convert γ-aminobutyrate to succinate-semialdehyde, which is then converted to succinate by succinate-semialdehyde dehydrogenase in the catabolism of γ-aminobutyrate. *See also* **4-aminobutyrate transaminase**.

succinic dehydrogenase *see* **succinate dehydrogenase (ubiquinone)**.

succinimide *a trivial name for* butanimide; 2,5-pyrrolidinedione; the imide of succinic acid. For structure *see* **+imide**.

succinoglycan an acidic exopolysaccharide needed for symbiosis between *Rhizobium meliloti* and alfalfa. Also synthesized by other bacteria, it is a polymer of octasaccharide subunits (one galactose and seven glucose residues) with acetyl, succinyl, and pyruvyl modifications.

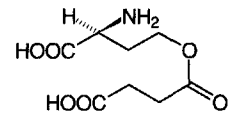
succinyl **1** *(in biochemistry) symbol*: Suc–; the univalent acyl group 3-carboxypropanoyl, HOOC–$[CH_2]_2$–CO–, derived from succinic acid by loss of one hydroxyl group. **2** *(in chemistry) symbol*: –Suc– *or* Suc<; the bivalent acyl group butanedioyl, –CO–$[CH_2]_2$–CO–, derived from succinic acid by loss of both hydroxyl groups.

succinylation the introduction of one or more **succinyl** (def. 1) groups into a substance by acylation, either chemically, e.g. with succinic anhydride, or enzymically, e.g. with succinyl-coenzyme A. Succinylation of a protein with succinic anhydride is used to acylate its free lysine (and other) amino groups in order to change their charge at neutral pH from positive to negative and to render adjacent peptide bonds resistant to hydrolysis by trypsin; it can also lead to disaggregation of a multimeric protein. The reaction occurs readily at pH 7–10 (at 0–25 °C), but it is irreversible, unlike the otherwise similar processes of **citraconylation** and **maleylation**, and so is of limited usefulness in protein sequence work.

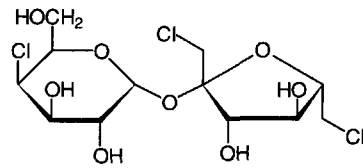
succinylcholine chloride *see* **suxamethonium**.

succinyl-CoA synthetase (GDP-forming) *see* **succinate–CoA ligase (GDP-forming)**.

***O*-succinylhomoserine** an intermediate in methionine biosynthesis in plants and bacteria. It is formed by succinylation (utilizing succinyl-CoA) of homoserine. It reacts with cysteine with loss of succinate to form cystathionine.



sucralose 4,1′,6′-trichloro-4,1′,6′-trideoxy-*galacto*-sucrose; a chlorinated sucrose, tasting sweeter than sucrose itself.



sucrase **1** *recommended name*: sucrose α-glucosidase; EC 3.2.1.48; *systematic name*: sucrose α-D-glucohydrolase; an α-D-glucosidase-type enzyme from intestinal mucosa that hydrolyses sucrose and maltose. It is also known as **sucrase–isomaltase** by virtue of its activity as an oligo-1,6-glucosidase, EC 3.2.1.10, displayed towards isomaltose. **2** *a former alternative trivial name for* **invertase**. **3** any of several bacterial or plant enzymes within sub-subclass EC 2.4.1 (hexosyltransferases) that synthesize various homopolysaccharides from sucrose by transfer of either its fructose moiety or its glucose moiety respectively to a fructan or to a glucan, with release of the opposing moiety as free D-glucose or D-fructose. The recommended names are formed by adding 'sucrase' to a prefix

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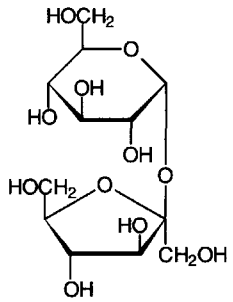
indicating the polysaccharide product. These enzymes include: (1) **amylosucrase**; EC 2.4.1.4; *other name*: sucrose–glucan glucosyltransferase; *systematic name*: sucrose:1,4-α-D-glucan 4-α-D-glucosyltransferase; it synthesizes amylose; (2) **dextransucrase**; (3) **inulosucrase**; EC 2.4.1.9; *other name*: sucrose 1-fructosyltransferase; *systematic name*: sucrose:2,1-β-D-fructan 1-β-D-fructosyltransferase; it synthesizes inulin; and (4) **levansucrase**; EC 2.4.1.10; *other name*: sucrose 6-fructosyltransferase; *systematic name*: sucrose:2,6-β-D-fructan 6-β-D-fructosyltransferase; it synthesizes levan.

sucrase-isomaltase *see* **oligo-1,6-glucosidase**.

sucrose *or* **saccharose** *the trivial name for* O-β-D-fructofuranosyl-(2→1)-α-D-glucopyranoside; a sweet-tasting, non-reducing disaccharide. The sugar of commerce, it is usually isolated industrially in crystalline form from sugar cane, *Saccharum officinarum*, or from sugar beet, *Beta vulgaris*.



sucrose gradient a density gradient made by mixing different concentrations of sucrose and layering them in a centrifuge tube. It is commonly used to separate molecules or particles on the basis of their sedimentation coefficients. *See also* **isopycnic centrifugation**.

sucrose-phosphate synthase EC 2.4.1.14; *systematic name*: UDPglucose:D-fructose-6-phosphate 2α-D-glucosyltransferase; *other names*: UDPglucose–fructose-phosphate glucosyltransferase; sucrosephosphate–UDP glucosyltransferase. An enzyme that catalyses a reaction between UDPglucose and D-fructose 6-phosphate to form sucrose 6-phosphate and UDP. Example from *Zea mays* (maize): database code SPS_MAIZE, 1068 amino acids (118.44 kDa).

sucrose phosphorylase EC 2.4.1.7; *systematic name*: sucrose:orthophosphate α-D-glucosyltransferase; *other name*: sucrose glucosyltransferase. An enzyme that catalyses the phosphorylysis of sucrose to D-fructose and α-D-glucose 1-phosphate. Example from *Leuconostoc mesenteroides*: database code LEUSUCP, 490 amino acids (55.68 kDa).

sucrose synthase EC 2.4.1.13; *systematic name*: UDP glucose:D-fructose 2α-D-glucosyltransferase; *other names*: UDPglucose–fructose glucosyltransferase; sucrose–UDP glucosyltransferase. An enzyme that catalyses a reaction between UDPglucose and D-fructose to form sucrose and UDP. Example, sucrose synthase 1 from *Hordeum vulgare* (barley): database code SUS1_HORVU, 807 amino acids (92.11 kDa).

Sudan the family name of a group of dyes that are soluble in organic solvents and are used for staining lipids. **Sudan Red** is the 2,2′-demethyl analogue of **Oil Red O**. **Sudan Black B** is used for staining chromosomes, Golgi apparatus, and leukocyte granules.

sugar *a general and imprecise name used for* any, usually sweet, soluble disaccharide or small oligosaccharide carbohydrate. More specifically it is applied to **sucrose**, the sugar of commerce. The name is also sometimes used as a synonym for **carbohydrate**. *See also* **beet sugar**, **blood sugar**, **cane sugar**, **corn sugar**, **fruit sugar**, **grape sugar**, **malt sugar**, **milk sugar**, **mushroom sugar**, **reducing sugar**.

sugar acid any **aldaric acid**, **aldonic acid**, or **uronic acid**.

sugar alcohol *an old name for* **alditol**.

sugar beet the plant *Beta vulgaris*, which has a large root with a high sugar content, for which it is extensively cultivated.

sugar transporter any of various transmembrane proteins responsible for sugar transport into cells. There are several mechanisms, and different superfamilies of proteins are involved, characteristically with five motifs. For example, **GTR1** causes facilitated diffusion of glucose, whereas XylE protein in *Escherichia coli* acts as an H^+–xylose symporter (*see* ***xylE***). Both belong to the 12-transmembrane domain superfamily. Other types include the **ABC transporter** type and **PTS** type. *See* **glucose transporter**.

suicide enzyme *see* **suicide repair (of DNA)**.

suicide inhibitor a type of enzyme inhibitor that is distinguished from a classical active-site-directed enzyme inhibitor in two key respects: (1) the inhibitor itself is relatively unreactive and becomes reactive only after interaction with the enzyme's active site; and (2) conversion to the active form depends on the specific catalytic capabilities of the active site, i.e. some part of the enzyme's normal catalytic capability is required. *See also* **photosuicide inhibitor**.

suicide repair (of DNA) a response in both bacteria and mammalian cells to a situation in which exposure to a nontoxic alkylation dose causes the rapid induction of enzymes that counter the mutagenic effect by removal of ***O*^{6}-methylguanine** formed by the alkylating agent. In the course of this repair reaction the methyl group is transferred to the enzyme, which is thereby inactivated (i.e. it is a **suicide enzyme**).

suicide substrate **1** a substrate that, in undergoing conversion by an enzyme, causes the enzyme to be modified in a way that permanently inactivates it. Hence the enzyme, by acting on the substrate, 'commits suicide'. **2** a compound that is converted by a metabolic pathway into an inhibitor of the pathway, as with the conversion of fluoroacetate to fluorocitrate. If the pathway is of sufficient importance, the cell thereby 'commits suicide'. *See also* **lethal synthesis**.

sulfa drug any member of a group of **sulfonamide** compounds that are clinically useful in the treatment of bacterial infections.

sulfamethoxazole 4-amino-*N*-(5-methyl-3-isoxalolyl)benzenesulfonamide; a **sulfonamide** antibacterial agent. As a mixture with **trimethoprim** it has the name **co-trimoxazole** (*proprietary names*: Bactrim; Septrim).

sulfane a chain of divalent sulfur atoms, as in hydrogen persulfide (HSSH) or polysulfanes (H_2S_x; e.g. H_2S_5 is pentasulfane).

sulfanilamide *p*-aminobenzenesulfonamide; *see* **sulfonamide**.

sulfatase *see* **arylsulfatase**.

sulfate *or (esp. Brit.)* **sulphate** the anion SO_4^{2-}.

sulfate adenylyltransferase EC 2.7.7.4; *other names*: sulfate adenylate transferase; ATP-sulfurylase; sulfurylase; an enzyme that catalyses the formation of **adenosine 5′-phosphosulfate** (adenylylsulfate) from ATP and sulfate with release of pyrophosphate. Example from *Escherichia coli*, two subunits: database code CYSD_ ECOLI, 302 amino acids (35.16 kDa); database code CYSN_ECOLI, 475 amino acids (52.50 kDa).

sulfatide a **galactosyl cerebroside** with a sulfate radical esterified at the 3′ position of the galactose moiety. Sulfatides are formed by **galactosylceramide sulfotransferase**.

sulfatide lipidosis *an alternative name for* **metachromatic leukodystrophy**.

sulfation factor a factor originally identified as promoting sulfate uptake by cartilage *in vitro*; it is now known as **somatomedin**.

sulfhemoglobin any of a group of poorly characterized derivatives of **hemoglobin**, often formed *in vivo* together with ferrihemoglobin. They are incapable of carrying oxygen and cannot be converted back to hemoglobin.

sulfhydryl *or* **thiol** the chemical group –SH; it is found in the amino acid **cysteine** and in other molecules. Two sulfhydryls can be oxidized to a disulfide bond, –S–S–.

sulfite *or (esp. Brit.)* **sulphite** the anion SO_3^{2-}.

sulfite reductase **1 sulfite reductase (NADPH)** EC 1.8.1.2;

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systematic name: hydrogen sulfide:$NADP^+$ oxidoreductase; the enzyme responsible for interconversion of hydrogen sulfide and sulfite in plants and most bacteria. It catalyses the reduction of sulfite, e.g. released from **3′-phosphoadenosine 5′-phosphosulfate** by thioredoxin. The reaction is:

$$H_2S + 3\ NADP^+ + 3\ H_2O = \text{sulfite} + 3\ NADPH;$$

cofactors are FAD, FMN, and siroheme. In plants and most microorganisms the H_2S reacts with *O*-acetylserine to form cysteine and acetate. The enzyme also oxidizes H_2S to sulfite. Example from *Thiocapsa roseopersicina*, two subunits; database code S34190, 522 amino acids (57.72 kDa); database code S34191, 561 amino acids (62.38 kDa). **2 sulfite reductase** EC 1.8.99.1; *systematic name*: hydrogen-sulfide:(acceptor) oxidoreductase. An iron-protein enzyme that catalyses the reaction:

$$H_2S + \text{acceptor} + 3\ H_2O = \text{sulfite} + \text{reduced acceptor}.$$

Example from *Archaeoglobus fulgidus*, two subunits: database code S27478, 418 amino acids (47.47 kDa); database code S27479, 366 amino acids (41.52 kDa).

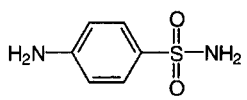
sulfmethemoglobin the complex formed by combination of sulfide with the ferric ion of **ferrihemoglobin** in poisoning by sulfide.

sulf(o)+ *or (esp. Brit.)* **sulph(o)+** of, or pertaining to, or containing a sulfur atom or group.

sulfokinase *or* **aryl sulfotransferase** EC 2.8.2.1; *other name*: phenol sulfotransferase; an enzyme that catalyses transfer of a sulfate radical from 3′-phosphoadenylylsulfate to a phenol to form an aryl sulfate.

sulfolipid any lipid containing sulfur, especially a **sulfatide**. *See also* **sulfonolipid**.

sulfonamide the amide of a sulfonic acid; the sulfonamide group is $-SO_2-NH_2$. In biology and medicine the name is used especially for any member of a large group of antibacterial substances – also known as **sulfa drugs** – derived from **sulfanilamide** (*p*-aminobenzenesulfonamide), many of which also have a substituent on the amide nitrogen.



sulfanilamide

sulfone the oxidation product that results when one oxygen atom is added to sulfur bonded to two alkyl chains.

sulfonolipid *or* **plant sulfolipid** 1,2-diacyl-3-(6-sulfo-α-D-quinovosyl)-*sn*-glycerol; sulfoquinovosyldiacylglycerol (*abbr.*: SQDG); the only sulfolipid present in higher plants and the only lipid with a sulfonic-acid linkage reported so far; the predominant fatty acid is α-linolenic acid. Sulfonolipid is localized in the chloroplasts, mainly in the membrane of the thylakoid system.

sulfoxide the oxidation product that results when two oxygen atoms are added to sulfur bonded to two alkyl chains.

sulfur *or (esp. Brit.)* **sulphur** *symbol*: S; a yellow nonmetallic element of group 16 of the IUPAC **periodic table**; atomic number 16; relative atomic mass 32.066. Its main oxidation states are –2, +4, and +6. Sulfur exists in a number of forms including crystalline (rhombic, monoclinic, rhombohedral) and amorphous forms. The relative abundance of stable isotopes is: sulfur-32 (mass 31.972) 95.02%; sulfur-33 (mass 32.971) 0.75%; sulfur-34 (mass 33.968) 4.21%. There are two radioactive isotopes, **sulfur-35** and **sulfur-38**. Sulfur is important as a constituent of the amino acids methionine and cysteine, and as a constituent of **glutathione**. It also occurs in **sulfolipids**. Sulfate is the terminal electron acceptor for anaerobic respiratory metabolism in certain bacteria e.g. *Desulfovibrio* spp.

sulfur-35 the radioactive nuclide, $^{35}_{16}S$, with a mass of 34.969. It emits an electron (β^- particle, 0.167 MeV), no gamma radiation, and has a half-life of 87.4 days.

sulfur-38 the radioactive nuclide, $^{38}_{16}S$, with a mass of 37.971. It emits an electron (β^- particle, 3.0 MeV) and gamma radiation (1.94 MeV), and has a half-life of 2.87 h.

sulfurylase *see* **sulfate adenylyltransferase**.

sulph(o)+ *a variant spelling (esp. Brit.) of* **sulf(o)+**.

sum **1** the total value of a set of individual values. **2** to determine a sum.

sumatriptan 3-[(2-dimethylamino)ethyl]-*N*-methyl-1*H*-indole-5-methanesulfonamide; a preferential agonist for $5\text{-}HT_{1D}$ receptors (*see* **5-hydroxytryptamine receptor**). It causes constriction of cerebral blood vessels, and is used in the treatment of migraine and cluster headaches. *Proprietary name*: Imigran (succinate).

summation the determination of the **sum** (def. 1) of a series.

Sumner, James Batcheller (1887–1995), US biochemist; Nobel Laureate in Chemistry (1946) 'for his discovery that enzymes can be crystallized' [prize shared with J. H. Northrop and W. M. Stanley].

SUMT *abbr. for* *S*-adenosyl-L-methionine:uroporphyrin-III *C*-methyltransferase (*see* **uroporphyrin-III *C*-methyltransferase**).

super+ *prefix* **1** above, over, at the top (of). **2** of greater size or extent, or of higher quality. **3** beyond the usual or normal standard; exceeding. **4** *(in chemical nomenclature)* designating a compound that contains more than the usual proportion of a specified element. *Compare* **sub+**, **supra+**.

superantigen an antigen with the ability to activate a large proportion (up to 20%) of T lymphocytes in a given individual through interaction with the variable domain of the β chain of the lymphocyte's antigen receptor. This contrasts with conventional foreign antigens the peptides of which, attached to the major histocompatibility complex (MHC), have to be specifically recognized by the T-cell receptor. With superantigens the specificity resides in the β chain of the receptor not the MHC peptides. This accounts for the fact that many more than usual T lymphocytes are activated. Superantigens are present in a number of bacteria and viruses; the best example is the *Staphylococcus* enterotoxin. Superantigens have been implicated in **autoimmunity**.

supercoil *or* **superhelix** *or* **coiled coil** the form of DNA that can be envisaged as resulting if a **duplex** were turned through a hairpin bend and the two duplex rails twisted one around the other. DNA *in vivo* generally is supercoiled, and as it has a closed structure, a supercoil may be envisaged as a rubber band twisted to a helical shape. In **negative supercoiling** the DNA twists around its axis in the opposite direction from the clockwise turns of the right-handed double helix; this allows relief of torsional pressure, and the DNA is said to be **underwound**. Twisting in the other direction (**positive supercoiling**) increases torsional pressure, winding the double helix more highly; the DNA is said to be **overwound**. **Superhelix density**, σ, is defined as the number of turns of the superhelix, τ, per turn of the duplex, β; i.e. $\sigma = \tau/\beta$ (β represents about 10 base pairs). **Linking number** is the number of times the duplex strands cross over each other (in projection onto a plane surface). The number of superhelical turns is called the **writhing number** (W).

supercritical fluid chromatography a technique that can be regarded as an extension of **gas–liquid (partition) chromatography** in which the mobile phase is a relatively dense gas such as CO_2 (or SF_6, NH_3, or Xe). The gas must be pumped (at pressures up to 6000 psi) through a capillary column that is coated with stationary phases similar to those used in gas chromatography. The system depends on the partition of the compounds being separated between the stationary and mobile phases and has the advantage that compounds with high boiling points partition appreciably into the gas phase at temperatures well below their boiling points so that such compounds can be separated at lower temperatures than with less dense gases.

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superfamily any group of genes and their cognate proteins that can be held to be related by sequence homology. The main criterion determining homology is conservation of residues that can be matched, if necessary, by alignment of the sequence. Normally, similarity of function is an additional criterion, but proteins apparently not related in function may be included if the degree of sequence homology is high. *See also* **Appendix E**.

superfolding (of proteins) the formation of small domains, beyond the level of simple secondary structures, that are energetically stable and contribute as units to the full tertiary structure of a protein. They may consist of **alpha helices** or **beta sheets** or both. Nine such protein folds have been identified in proteins having neither sequence nor functional similarities. In the folding of a protein, they may be formed initially before the protein fully folds. **Beta barrels** represent an example.

superfusion **1** the pouring of a liquid onto or over something. **2** *(in physiology and medicine)* a technique in which blood, plasma, or other fluid is allowed to drip onto, or flow over, the surface of an organ or piece of tissue.

supergene a group of linked genes (*see* **linkage** (def. 1)) that are usually inherited as a unit.

superhelix *an alternative name for* **supercoil**.

superhelix density *see* **supercoil**.

superinfection the proliferation of one or more pathogenic microorganisms arising from the disturbance of a mixed population of microorganisms normally sustained at non-pathogenic levels by secretion of endogenous antibiotics. Such disturbance can be induced by administration of exogenous antibiotic agents.

superinfection inhibition interference with the entry or establishment of an entering plasmid by a resident plasmid.

supernatant **1** floating on the surface of a liquid or lying over something. **2** (*or* **supernate**) **a** liquid lying above another liquid, a sediment, or a settled precipitate. **b** the fluid phase that remains after removal of solid material by centrifugation. A **cell supernatant** is the fluid phase that remains after centrifugation of a cell homogenate at high speed (characteristically at 100 000*g* for 30 min). *Compare* **infranatant**.

supernate *an alternative name for* **supernatant** (def. 2).

superoxide **1** the anion, O_2^-, formed by addition of one electron to **dioxygen**. **2** any compound containing the superoxide anion.

superoxide dismutase *abbr.*: SOD; EC 1.15.1.1; *systematic name*: superoxide:superoxide oxidoreductase; *other names*: cytocuprein; erythrocuprein; hemocuprein. Any of a group of metal-containing enzymes that bring about the **dismutation** of superoxide radicals to form dioxygen and hydrogen peroxide as follows:

$$O_2^{-}\bullet + O_2^{-}\bullet + 2H^+ = O_2 + H_2O_2.$$

It is important in removing the highly toxic superoxide radical. Some (e.g. those from *Neurospora*, yeast, erythrocytes, heart, peas) contain copper and zinc; others (e.g. those from *Escherichia coli*, *Streptomyces mutans*) contain manganese or iron. Eukaryotic cells have copper–zinc types in cytoplasm and manganese types in mitochondria. The copper–zinc types comprise a well-conserved family with four motifs. Examples: (1) copper–zinc type (bovine): database code NRL_2SODO, 151 amino acids (15.53 kDa); 3-D structure known; (2) manganese type (heterodimer) from human; chain A: database code NRL_1MSDA, 198 amino acids (22.18 kDa); 3-D structure known; chain B: database code NRL_1MSDB, 198 amino acids (22.18 kDa); 3-D structure known; (3) iron type (heterodimer) from *Pseudomonas putida*; chain A: database code NRL_3SDPA, 186 amino acids (20.47 kDa); 3-D structure known; chain B: database code NRL_3SDPB, 186 amino acids (20.47 kDa); 3-D structure known.

supported reagent any reagent linked to a **support medium**.

support medium any (usually solid or insoluble) medium to which a cell, reagent, or functional group can be attached.

suppression **1** *(in molecular biology)* the cancellation, or reversal of the effects, of one mutation by another mutation, except where the second mutation causes a single base change at the same point as an earlier **point mutation** (in which case the term **reversion** is used). In **intergenic suppression**, the effects of a mutation in one gene are reversed by a mutation in another gene, usually because the second gene codes for a mutant tRNA (*see* **frameshift suppressor**). In **intragenic suppression** a mutation is cancelled by a second mutation close to the first in the same gene, normally within the same triplet, giving rise to a codon that is compatible with translation to a functional protein product. As an example, if the first mutation changed AGT (leading to the RNA codon for Ser) to ATT (giving a nonsense codon), a suppressor mutation might change the triplet to ATA (giving the RNA codon for Tyr); if the change Ser to Tyr led to a functional protein, suppression would be achieved. *See also* **amber suppressor**, **ochre suppressor**, **opal suppressor**. **2** *(in immunology)* any attenuation of an immune response. The existence of a subpopulation of T cells, **suppressor cells**, is held to be responsible for attenuation of the effect of **helper cells**. A different mechanism is probably responsible for the reduction in antibody production arising from injection of antibody prior to administration of antigen. Allotype suppression refers to suppression of the production of one allotype (e.g. expression of the allotype inherited from the mother, and suppression of the allotype of the father).

suppressor cell *or* **suppressor T cell** *or* **T-suppressor cell** any of a subset of **T lymphocytes** that exert a negative regulatory effect (*see* **suppression** (def. 2)) on the stimulation of the immune response by **helper cells**. Classically they belong to the **CD8⁺** subset in the human. Induction of the suppressor function may derive from helper cells.

suppressor gene a gene that by its presence can reverse the effect of a specific type of mutation in another gene. *See* **suppression** (def. 1).

suppressor mutation a secondary mutation that totally or partially restores a function lost due to a primary mutation at another locus. *See* **suppression** (def. 1).

suppressor tRNA any species of **transfer RNA** (tRNA) that recognizes a **termination codon** in messenger RNA. It adds an amino-acid residue to what is normally the C terminus of a nascent polypeptide chain; hence termination of synthesis of the peptide is suppressed and a **readthrough** protein is consequently formed. Suppressor tRNA may occur naturally or be produced by mutagenesis.

supra+ *prefix* above, over, greater than. *Compare* **infra+**, **super+**.

supramolecular describing any chemical system or component thereof that exists and functions at a higher level of complexity than intact individual molecules. In biochemistry the term may refer to multienzymes, microtubules, organelles, biological membranes, viral envelopes, cell walls, ribosomes, or other cellular elements; hence, e.g., supramolecular assembly, supramolecular complex, supramolecular structure. *Compare* **submolecular**.

suprarenal gland *an obsolete term for* **adrenal gland**.

suprarenin *a former name for* adrenaline (i.e. **epinephrine**).

Sur *symbol for* a residue of the thiopyrimidine base **thiouracil**.

surface-active agent *an alternative term for* **surfactant**.

surface concentration *see* **concentration** (def. 1).

surface-stress theory a theory that considers the problem of mechanical stress in relation to enlargement of the bacterial cell wall during growth. The cell wall withstands stress from hydrostatic pressure by a stress-bearing, two-dimensionally linked peptidoglycan sacculus that surrounds the cell. During enlargement, enzymes that enlarge the wall must at the same time maintain the hydrostatic integrity of the cell by withstanding stress.

surface tension *symbol*: Y *or* σ *or* γ; the property that makes a liquid behave as if it had an elastic skin on its surface – at an interface with a gas or an immiscible liquid – as a result of intermolecular forces tending to pull the molecules in the sur-

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face into the interior of the liquid. It is defined as the force acting tangential to the surface on one side of a line of unit length in the surface, and is expressed in newtons per metre. It can also be defined as the work required to produce unit increase in surface area, expressed in joules per square metre.

surfactant *or* **surface-active agent** any substance, such as a **detergent** or an **emulsifier**, that can bring about a reduction of the **surface tension** of a liquid, allowing it to foam, to penetrate porous solids more easily, and to wet surfaces of nonporous solids or of immiscible liquids.

surfactin a surface-active antibiotic and nonimmunogenic hemolysin produced extracellularly by *Bacillus subtilis*. It consists of a nonapeptide (containing *inter alia* two residues each of L- and D-leucine) in cyclic depsipeptide linkage with β-hydroxy-ω-methylmyristic acid.

surrogate genetics a branch of molecular genetics in which DNA is modified *in vitro* and then reintroduced into a genetic system – the 'surrogate' system – e.g. by injection into *Xenopus* oocytes, by transfection of cells, or by the creation of transgenic animals. The effect of the modification on the expression of the gene provides insights into the role in the genetic system of particular base sequences.

surveyor substrate one of a system of fluorescent substrates designed to measure distances within the active centre of an enzyme and also to survey other aspects of the topography of the active centre during the catalytic event.

survivin a protein expressed in the G_2/M phase of the cell-division cycle that associates with microtubules of the mitotic spindle. It inhibits **apoptosis**.

Sushi domain a polypeptide domain of approximately 60 amino acids that contains disulfide bonds between the first and third and second and fourth cysteines, as found in β_2 glycoprotein-1 of plasma, in complement proteins, and in **blood coagulation** factor XIII.

suspension culture the culture of cells in medium without adherence to a stationary substrate. Relatively few animal cell types are amenable to suspension culture (classically **HeLa cells** can be so grown). An intermediate situation utilizes beads to which the cells adhere; the beads can be maintained in suspension and collected by sedimentation

Sutherland, Earl Wilbur Jr (1915–74), US biochemist; Nobel Laureate in Physiology or Medicine (1971) 'for his discoveries concerning the mechanisms of the action of hormones'; these included the discovery of cyclic AMP.

suxamethonium succinylcholine chloride, 2,2′-[(1,4-dioxo-1,4-butanediyl)bis(oxy)]bis[*N*,*N*,*N*-trimethylethanaminium] dichloride; a nicotinic receptor ligand that causes sustained activation of the receptors leading to blockade of synaptic transmission ('depolarizing block'). It is used as a neuromuscular blocking agent in surgery. It acts by mimicking acetylcholine at the neuromuscular junction, but disengagement from the receptor site and subsequent breakdown are slower than for acetylcholine. It is hydrolysed by serum cholinesterase and recovery is spontaneous. **Decamethonium** was the first drug of this type to be developed. Both of these compounds depend for their action on the N^+–N^+ distance of 1.1 nm. *Compare* **curare**, **tubocurarine**.

Sv *symbol for* **1** sievert. **2** svedberg (alternative to S).

SV40 *abbr. for* simian virus 40.

svedberg *or* **Svedberg unit** *symbol*: S *or* Sv; a coherent non-SI unit used as a measure of **sedimentation coefficient**; 1 S = 10^{-13} s.

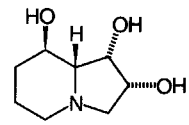
Svedberg, Theodor (1884–1971), Swedish colloid chemist noted for his invention (in 1923) of the ultracentrifuge; Nobel Laureate in Chemistry (1926) 'for his work on disperse systems'.

Svedberg centrifuge a centrifuge, designed and built by **Svedberg** in 1923, that was the forerunner of the **ultracentrifuge**.

Svedberg equation an equation relating the relative molecular mass, M_r, of a solute to its sedimentation velocity in an applied centrifugal field. If s is the sedimentation coefficient, D is the diffusion coefficient, $\bar{v}$ is the partial specific volume of the solute, ρ is the density of the solution, R is the gas constant, and T is the thermodynamic temperature, then

$$M_r = sRT/D(1 - \bar{v}\rho),$$

swainsonine 8α,β-indolizidine-1α,2α,8β-triol; an inhibitor of a number of α-mannosidases, particularly Golgi mannosidase II (*see* **Golgi mannosidase**), an important enzyme in the synthesis of the core oligosaccharide of a number of membrane glycoproteins. It inhibits the growth of tumours and prevents metastases in mice. [After its source, *Swainsona canescens*].



swaposin a form of protein homology in which domains, characteristically found in one protein, are found arranged in other proteins in a different order. The phenomenon was first commented on in relation to certain plant aspartic peptidases, which contain saposin-like domains swapped into a different order to that found in **saposins** (hence the name). In another example some **pleckstrin homology domains** are found to be interrupted by inserts of **SH domains**.

sweetener any compound intended as a substitute for sucrose in sweetening food or drink, and aimed at avoiding the possible harmful effects of sucrose. Such compounds therefore should be nonnutritive but with a taste and aftertaste similar to those of sucrose; they should also be nonharmful. They include **aspartame**, **lactitol**, **mannitol**, **monellin**, **saccharin**, **stevioside**, **sucralose**, and **volemitol**. Sodium cyclamate was used as a sweetener until it was banned in the USA in 1970 because of its carcinogenicity.

sweetness one modality of the sense of taste, characterized by the effect of certain sugars such as sucrose and fructose.

swinging-bucket rotor a type of centrifuge head in which the centrifuge tubes are placed in buckets that swivel on trunnions so that at speed the tube is oriented with its axis parallel to the centrifugal force (i.e. horizontal). Such a head is essential for zonal centrifugation through density gradients as angled tubes induce mixing. *Compare* **angle head**.

SwissProt a protein sequence database maintained by the University of Geneva. It contains sequences of many proteins and references to articles in which the sequences were reported, together with a limited amount of general information and the name of the gene that encodes the protein.

switch peptide the flexible covalent connection between the **variable region** and **constant region** of an immunoglobulin molecule.

switch recombinase *see* **homothallic switching endonuclease**.

swivelase *see* **DNA swivelase**.

SYBASE a relational database used, e.g., for **HUGO**.

sym+ *a variant form of* **syn+** (before b, m, or p).

sym- *prefix (in chemical nomenclature)* denoting symmetric; e.g. *sym*-trinitrobenzene.

symbiont an organism that lives as a partner in a **symbiosis**.

symbiosis (*pl.* **symbioses**) a long-term association between individuals belonging to two different species. The term is often used in a restricted sense to denote associations that are beneficial to one or both partners, although strictly it refers equally to neutral or harmful associations. —**symbiotic** *adj.*

symmetry precise correspondence between two halves with respect to both size and shape. A molecule has an *n*-fold **axis of symmetry** if rotation around this axis through an angle of 360°/*n* produces an arrangement indistinguishable from the original (*n* being a small integer). For example, water has a twofold (n = 2) axis of symmetry. A plane of symmetry is a plane drawn through a molecule such that a mirror placed in

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this plane forms an image of one half of the molecule that is superimposable on the other half. For example, a plane of symmetry is present in *meso*-**tartaric acid**. An alternating axis of symmetry or rotation–reflection axis is an axis such as is present in a molecule when rotation around the axis through an angle of 360°/*n* followed by reflection in a plane perpendicular to the axis produces a molecule superimposable on the original molecule. For example, a compound with such a twofold ($n = 2$) axis is fumaric acid. A centre of symmetry is a position (point) such that if a straight line is drawn from every atom to the point, and is continued beyond the point, an equivalent atom is found at a distance equal to that between the point and the original atom. A molecule with such a centre has a twofold alternating axis of symmetry. An example of a molecule with a centre of symmetry is fumaric acid.

sympathectomy the surgical section of sympathetic nerve fibres.

sympathetic nervous system one of the two divisions of the **autonomic nervous system** the other being the parasympathetic nervous system. Most, but not all, sympathetic nerves release **norepinephrine** as a neurotransmitter.

sympatheticomimetic *an alternative term for* **sympathomimetic**.

sympathomimetic *or* **sympatheticomimetic** **1** describing a substance or action that stimulates the **sympathetic nervous system**; **adrenergic**. **2** a sympathomimetic agent, especially a sympathomimetic amine.

symport *or* **cotransport** the process of solute translocation in which two solutes equilibrate across an osmotic barrier, and the translocation of one solute is coupled to the translocation of the other in the same direction. *Compare* **antiport**.

symporter any substance or structural feature that promotes the exchange diffusion of two specific substances across a membrane by **symport**.

syn- *abbr. for* synclinal (def. 1); *see also* **conformation**.

syn+ *comb. form* signifying similarity, association, or concerted action.

Synacthen *see* **tetracosactide**.

synaeresis *a variant spelling of* **syneresis**.

synapse *or (rare)* **synapsis** the junction between a nerve fibre of one neuron and another neuron; the site of interneuronal communication. As the nerve fibre approaches the synapse it enlarges into a specialized structure, the **presynaptic nerve ending**, which contains mitochondria and **synaptic vesicles**. At the tip of the nerve ending is the **presynaptic membrane**; facing it, and separated from it by a minute cleft – the **synaptic cleft** – is a specialized area of membrane on the receiving cell, known as the **postsynaptic membrane**. In response to the arrival of nerve impulses, the presynaptic nerve ending secretes molecules of **neurotransmitters** into the synaptic cleft. These diffuse across the cleft and transmit the signal to the postsynaptic membrane. *See also* **neuromuscular junction**. —**synaptic** *adj.*

synapsin I a major neuron-specific protein present in virtually all synaptic vesicles. Phosphorylated at multiple sites by Ca^{2+}-calmodulin-dependent and cyclic AMP-dependent protein kinases, it coats synaptic vesicles and binds to the cytoskeleton. Example, precursor for human synapsin IA: database code SYN1_HUMAN, 705 amino acids (73.92 kDa); synapsin IB is derived by alternative splicing; synapsins II are related.

synapsis **1** the pairing of chromosomes during **meiosis**. **2** *a less common word for* **synapse**.

synaptic cleft the extracellular space, typically some 20 nm across, that separates the outer membrane of the presynaptic nerve ending from the postsynaptic membrane of the receiving neuron (or other target cell) in a **synapse**. Chemical mediation of nerve transmission occurs across the synaptic cleft.

synaptic vesicle a vesicle, 20–65 nm in diameter, occurring within the cytoplasm of the presynaptic nerve ending and often closely related to the presynaptic membrane (*see* **synapse**). Synaptic vesicles store **neurotransmitters** and release them by fusing with the presynaptic membrane.

synaptic vesicle-associated membrane protein *another name for* **synaptobrevin**.

synaptobrevin *or* **sinaptobrevin** *or* **synaptic vesicle-associated membrane protein** (*abbr.*: VAMP) a SNAP receptor involved in the docking and fusion complex (*see* **SNARE**) of synaptic vesicles and playing a central role in neural exocytosis. Synaptobrevin isoforms 1 and 2 (VAMP-1 and VAMP-2) are known. Both are expressed in all the main rat tissues, but differential expression is found, e.g. VAMP-1 is restricted to exocrine pancreas and kidney tubular cells, VAMP-2 predominates in islets of Langerhans and kidney glomerular cells. Example from *Drosophila melanogaster* (similar to fish and mammalian proteins): database code SYB_DROME, 152 amino acids (16.69 kDa).

synaptojanin a protein found in brain in nerve terminals, that has inositol 5-phosphatase activity and binds to the SH3 domain of **amphiphysin**, colocalizing with that protein in double immunofluorescence micrographs. It appears to participate with **dynamin** in synaptic vesicle recycling. It has homology with the yeast protein Sac1, which is genetically implicated in phospholipid metabolism and the function of the actin cytoskeleton. mRNA sequence from *Rattus norvegicus*: database code RNU45479.

synaptonemal complex a structure that holds paired chromosomes together during prophase I of **meiosis** and that promotes genetic recombination.

synaptophysin an integral membrane glycoprotein that occurs in presynaptic vesicles of neurons and in similar vesicles of the adrenal medulla. A marker protein for neuroendocrine cells and neoplasms, it has the attributes of a vesicular channel protein. Example from rat: database code SYNP_RAT, 265 amino acids (29.03 kDa).

synaptosome any of the discrete particles (nerve-ending particles) formed from the clublike presynaptic nerve endings that resist disruption and are snapped or torn off their attachments when brain tissue is homogenized in media isosmotic to plasma. In synaptosomes the main structural features of the nerve endings are preserved.

synaptosome-associated protein *see* **SNAP** (def. 2).

synaptotagmin an abundant integral membrane protein of synaptic vesicles and chromaffin granules with a proposed role in membrane interactions during trafficking of synaptic vesicles at the active zone of the synapse. The primary structure contains two copies of a repeat that is homologous to the regulatory domain of protein kinase C. Example, homotetramer, human synaptotagmin I (*other name*: p65): database code SYT1_HUMAN, 422 amino acids (47.52 kDa).

synarchic regulation *see* **synarchy**.

synarchy cooperation between two intracellular messengers (e.g. cyclic AMP and Ca^{2+}) that act in concert to activate intracellular pathways.

syncatalytic synchronous with the catalytic process.

synchrotron an apparatus used in nuclear physics that accelerates particles of atomic size through an electric field. The particles are initially charged by an ion source, and their path may be linear (**linear accelerator**) or of spiral form (**cyclotron**). The acceleration imparts a high kinetic energy to the particles, which can lead to structural changes in the particles. One use of a synchrotron, therefore, is the production of radioactive or other nuclides for use in biology or medicine. A synchrotron radiation source is a circular storage ring in which electrons are accelerated in a magnetic field.

synclinal **1** *abbr.*: *syn-*; describing one of the two possible conformations of the base and sugar ring in a nucleotide, the other being the **anticlinal** conformation. *See* **conformation**. **2** *or (sometimes)* **gauche** *or* **skew** *abbr.*: *sc-*; describing a particular staggered conformation of a molecule in which the **torsion angle** is within ±60° of 0°. *See* **conformation**.

syncytium (*pl.* **syncytia**) a mass of cytoplasm containing several nuclei enclosed within a single plasma membrane. Syncytia are normally derived from single cells that fuse or fail to

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complete cell division. Examples are muscle fibres, formed by fusion of **myoblasts**, and residual bodies formed during **spermatogenesis**.

SYND2 *abbr. for* syndecan-2. *See* **syndecan**.

syndecan a type I integral membrane proteoglycan that links the cytoskeleton to the interstitial matrix. It bears heparan sulfate and chondroitin sulfate and binds to bFGF (*see* **fibroblast growth factor**) with high affinity, and also to components of the extracellular matrix. Its intracellular domain binds to the actin cytoskeleton. Examples (precursors) from human, syndecan-1: database code SDC1_HUMAN, 310 amino acids (32.44 kDa); syndecan-2 (*abbr.*: SYND2); (*other names*: fibroglycan; heparan sulfate proteoglycan core protein; (*abbr.*: HSPG); database code SDC2_HUMAN, 201 amino acids (22.15 kDa).

syndein *an alternative name for* **ankyrin**.

syndesine a di(α-amino acid) isolated from hydrolysates of certain **collagens**, in which it forms covalent cross-links between adjacent polypeptide strands. It is formed by **aldol condensation** between the side chains of a residue of **allysine** and one of **hydroxyallysine**; two isomers are possible.

syndiotactic having or relating to a regular alternation of differences in stereochemical structure in the repeating units of a polymer. *Compare* **isotactic**.

syndiotactic polymer a regular polymer composed of molecules having a regular repetition of alternating enantiomeric configurational base units at least at one main-chain chiral or prochiral atom in the configurational base unit.

syndrome a set of concurrent symptoms characteristic of a particular pathological state.

synemin a protein, M_r 230 000, that is found in the Z disk of skeletal and cardiac muscle cells and in **intermediate filaments** of some nonmuscle cells. It binds tightly to **desmin**.

synenkephalin or **proenkephalin 1–70** a derivative of **proenkephalin** secreted as an intact molecule or as a part of precursors in the adult brain and adrenal medulla. It has the immunoreactivity of proenkephalin but does not contain the enkephalin sequence.

syneresis *or* **synaeresis** **1** *(in chemistry)* the separation of liquid from a gel caused by contraction of the gel structure. **2** *(in pathology)* the gradual contraction of a blood clot that occurs after its formation, leading to a more solid mass that seals the ruptured blood vessel.

synergism **1** the phenomenon whereby the effect of two or more agonists together is greater than the sum of their effects when used individually. **2** the concerted action of two muscles to enhance their combined effects. *Compare* **antagonism**. —**synergetic** *or* **synergistic** *adj.*

synergist **1** an agent that increases the effectiveness of another agent. **2** a muscle that acts in concert with another muscle to increase its effect. *Compare* **antagonist**.

synexin *or* **annexin VII** a cytosolic Ca^{2+}-dependent lipid-binding protein belonging to the **annexin** family. Originally isolated from adrenal medullary cells, isoforms have since been found in skeletal muscle, brain, and liver, and also in *Dictyostelium discoideum*. Adrenal medulla and liver have isoforms of 47 kDa and 51 kDa, while skeletal muscle has only the 51 kDa isoform. Synexin promotes membrane fusion, aggregates isolated chromaffin granules, and forms voltage-dependent calcium channels in artificial and natural membranes.

syngamy the union of the nuclei of two gametes to form the single nucleus of the zygote during fertilization; sexual reproduction. —**syngamic** *or* **syngamous** *adj.*

Synge, Richard Laurence Millington (1914–94), British biochemist and peptide chemist; Nobel Laureate in Chemistry (1952) jointly with A. J. P. Martin 'for their invention of partition chromatography'.

syngeneic of or pertaining to cell types in an experimental mammalian chimera that are antigenetically similar. *Compare* **allogeneic**.

synonym codon a **synonym triplet** in messenger RNA.

synonymous mutation *an alternative name for* **silent mutation**.

synonym triplet any of the two or more sequences of three purine and/or pyrimidine bases in nucleic acids that may specify the same amino acid. In messenger RNA the term is synonymous with **synonym codon**.

synovia *or* **synovial fluid** the fluid surrounding a joint or filling a tendon sheath.

synovial membrane *or* **synovium** the membrane of mesothelial cells and connective tissue that surrounds a joint; it secretes the **synovia**.

synovium *an alternative name for* **synovial membrane**.

synperiplanar *see* **conformation**.

syntaxin a SNAP receptor (**SNARE**) involved in docking of synaptic vesicles at the presynaptic zone of a **synapse**. Example, syntaxin A from rat: database code SYNA_RAT, 288 amino acids (33.03 kDa).

syntenic genes gene loci or genes that lie on the same chromosome.

synthase a generic name that may be added to the name of a substance to designate an enzyme catalysing a reaction in which the named substance is synthesized. The synthases are distributed amongst various systematic classes of enzymes – e.g. glycogen synthase is in class EC 2 and malate synthase is in class EC 4 – although until 1984 no enzyme of class EC 6 (ligases) could be so named. Now the term is used also to form the recommended names of a few enzymes where the reaction is complex and there is a common name for the product (e.g. EC 6.3.2.11, carnosine synthase). The majority of enzymes in the EC 6 class now have recommended names ending in ligase, e.g. EC 6.5.1.3, RNA ligase (ATP), which has also been termed polyribonucleotide synthase (ATP). In the past, the term synthase was frequently used interchangeably with **synthetase**.

synthase–phosphorylase kinase EC 2.7.1.37; *recommended name*: protein kinase; *other names*: phosphorylase *b* kinase kinase; glycogen synthase *a* kinase; hydroxyalkyl-protein kinase; serine(threonine) protein kinase. A serine/threonine **protein kinase** that catalyses phosphorylation of several proteins as indicated by the names above; it is activated by phosphorylation by **cyclic AMP-dependent protein kinase**. In addition to regulating the glycogen phosphorylase/synthase enzymes, it can activate the ATP,Mg^{2+}-dependent (AMD) protein phosphatase and other proteins. Example, GSK-3 (rat), a serine protein kinase implicated in the hormonal control of several regulatory proteins including glycogen synthase, Myb protein, and the transcription factor product of c-*jun*; monomer: database code KG3B_RAT, 420 amino acids (46.69 kDa). *See also* **phosphorylase kinase**.

synthesis *(in chemistry)* the production of a more complex molecule from simpler reagents by one or a series of reactions. —**synthesize** *or* **synthesise** *vb.*

synthesizer *or* **synthesiser** an instrument that automates a chemical synthesis, especially of peptides or oligonucleotides.

synthetase **1** an old class name, still widely used but no longer recommended, for any enzyme of class EC 6; these enzymes are now classified under the systematic class name **ligase**. **2** a generic name that may be added to the name of a substance to form the common name of any ligase-class enzyme that catalyses a reaction producing the named substance with concomitant breaking of a diphosphate linkage in a nucleoside triphosphate; e.g. acetyl-CoA synthetase (EC 6.2.1.1, acetate–CoA ligase), glutamine synthetase (EC 6.3.1.2, glutamate–ammonia ligase is recommended). Until 1984 names so formed were often the recommended names of such enzymes; now, the generic names ligase or **synthase** are used to form the recommended names, although common names formed from synthetase are still acceptable. In the past, the term synthetase was frequently used interchangeably with synthase.

synthetic **1** of, or pertaining to, **synthesis**. **2** (of a substance or material) chemically synthesized as opposed to prepared from recognizable natural materials. Such a product is identical chemically to that isolated from the natural source.

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synuclein a brain presynaptic protein that is expressed also in other tissues, but at very low levels. It is highly conserved, rodent and zebrafish α synucleins being 95% and 86% identical to human. Some mutations are linked to familial **Parkinson's disease**. Example: SYUA_HUMAN, 140 amino acids (14.46 kDa).

synxenic pertaining to the growth of organisms of a single species in the presence of one or more other species. A culture in which one other species is involved is described as **monoxenic**; with two other species it is **dixenic**; and with three it is **trixenic**. Cultures with more than three additional species are described as **polyxenic**. *Compare* **axenic**. —**synxenity** *n.*; **synxenize** *or* **synxenise** *vb.*

synxenite the principal organism being studied in a **synxenic** culture.

syrup *or* **sirup** **1** a thick, sticky, viscous liquid consisting of a concentrated aqueous solution of sucrose. **2** the concentrated juice of a fruit or plant, especially of sugar cane. **3** any solution that is thick, sticky, and viscous.

system A one of the transport systems responsible for the uptake of neutral amino acids by animal cells. It is most reactive with amino acids having short, polar or linear side chains, including the nonmetabolizable 2-aminoisobutyric acid. Transport is sodium ion-dependent and is reduced by lowered extracellular pH. **System ASC**, prominent in erythrocytes, is distinguished from system A on the basis of pH insensitivity and higher stereospecificity. *See also* **sodium/neutral amino acid cotransporter**, **system L**, **system N**.

system ASC *see* **system A**.

systematic name **1** *(in organic-chemical nomenclature)* a name of a molecular entity that is composed wholly of specially coined or selected syllables, with or without numerical affixes and locants; e.g. oxazole, pentane, cyclohex-2-en-1-ol. Such a name unequivocally specifies the complete chemical structure of a particular molecular entity. *Compare* **semisystematic name**, **trivial name**. **2** *(in enzyme nomenclature)* a name of an enzyme that describes its catalytic action as exactly as possible, thus identifying the enzyme precisely. Such names are formed in accordance with definite rules, which provide the basis for classifying enzymes according to the type of reaction catalysed and for assigning code numbers to them. One important consequence of this method of classifying is that, with certain exceptions, all proteins having the same catalytic property share the same systematic name and code number irrespective of their source and structure. To simplify classification, the direction of the reaction catalysed is chosen to be the same for all enzymes in a given class, even if only the reverse reaction has been actually demonstrated experimentally for a particular enzyme. A systematic enzyme name consists of two parts: the first contains the name of the substrate or, in the case of a bimolecular reaction, of the two substrates separated by a colon (with small and equal spaces before and after the colon); and the second, ending in '+ase', indicates the nature of the catalysed reaction.

systematics *functioning as sing.* **1** the study of systems, especially the principles of classification. **2** *(in biology)* the discipline that deals with classification and nomenclature.

Système International *abbr.*: SI; Système International d'Unités; a system of units based on the metric system. *See* **SI units**.

systemic concerning the whole body of an animal or a whole plant rather than an individual part.

systemic circulation the blood vessels supplying all parts of the body except the lungs.

systemin an 18-residue polypeptide, isolated from tomato leaves, that acts as a potent activator of plant proteinase inhibitor genes. It induces synthesis of two proteinase inhibitors in tomato and potato leaves. It is the only plant polypeptide hormone-like signalling molecule presently known. It has the sequence

AVQSKPPSKRDPPKMQTD,

and is proteolytically processed from a 200-residue precursor, **prosystemin**. Example: database code SYST_LYCES, 200 amino acids (23.00 kDa). Plant proteinase inhibitors are induced by wounding, e.g. by insects or pathogens, and may be part of the plant defence mechanisms.

system L one of the transport systems responsible for the uptake of neutral amino acids by animal cells. It is most reactive with branched-chain and aromatic amino acids such as leucine, isoleucine, valine, phenylalanine, and the nonmetabolizable analogue 2-aminobicyclo-[2,2,1]-heptane-2-carboxylic acid (BCH). The transport mechanism is sodium-ion-independent and may be stimulated by lowered extracellular pH. System L has been described in a wide variety of animal cell types, including avian and mammalian. Example from *Pseudomonas aeruginosa*: database code BRAZ_PSEAE, 437 amino acids (45.27 kDa). *See also* **sodium/neutral amino-acid cotransporter**, **system A**, **system N**.

system N one of the transport systems responsible for the uptake of amino acids by animal cells. It is a sodium-ion-dependent system specific to asparagine, glutamine, and histidine. *See also* **sodium/neutral amino acid cotransporter**, **system A**, **system L**.

systole a rhythmical repeated contraction, as of the chambers of the heart or of a pulsating vacuole. *Compare* **diastole**. —**systolic** *adj.*

Szent-Györgyi **Albert Szent-Györgyi von Nagyrapolt** (1893–1986), Hungarian-born US biochemist distinguished for his work in a variety of fields, including the isolation of ascorbic acid, the role of dicarboxylic acids in oxidative metabolism, and the biochemistry of muscle contraction; identified **adenylic acid**; Nobel Laureate in Physiology or Medicine (1937) 'for his discoveries in connection with the biological combustion processes, with special reference to Vitamin C and the catalysis of fumaric acid'.

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Tt

t 1 *symbol for* **a** tert+ (i.e. **tertiary**) in a chemical name (alternative to *t*). **b** **triton** (def. 2). **2** *abbr. for* terminator sequence.

t *symbol for* **1** time. **2** Celsius temperature (alternative to θ). **3** transference number.

t- *abbr. for* **1** *tert-*. **2** *trans-*.

$t_{½}$ *symbol for* half-life. *See also* $T_{½}$.

T *symbol for* **1** tera+ (SI prefix denoting 10^{12} times). **2** tritium. **3** tesla. **4** a residue of the α-amino acid L-threonine (alternative to Thr). **5** a residue of the base thymine in a nucleic-acid sequence. **6** a residue of the ribonucleoside ribosylthymine (*not* thymidine, i.e. deoxyribosylthymine; alternative to Thd). **7** twist number.

T *symbol for* **1** thermodynamic temperature. **2** transmittance. **3** period. **4** kinetic energy (alternative to E_K or K).

-*T* conformational descriptor designating the **twist conformation** (def. 2) of a five-membered ring form of a monosaccharide or monosaccharide derivative. Locants of ring atoms that lie on the side of the structure's reference plane from which the numbering appears clockwise are indicated by left superscripts and those that lie on the other side of the reference plane are indicated by right subscripts; e.g. 1,2-*O*-isopropylidene-β-L-ido-furanose-$^3T_2$. *See also* **conformation**.

$T_{½}$ *symbol for* half-life of a radionuclide (alternative to $t_{½}$).

T_1 *symbol for* spin-lattice relaxation time, longitudinal relaxation time.

T_2 *symbol for* spin-lattice relaxation time, transverse relaxation time.

T_m *or* t_m *or* Θ_m *symbol for* melting temperature.

T_t *symbol for* transition temperature.

T1 *abbr. for* bacteriophage T1, a **T-odd phage**.

T2 **1** *or* T_2 *symbol for* L-diiodothyronine. **2** *abbr. for* bacteriophage T2, a **T-even phage**.

T3 **1** *or* T_3 *symbol for* L-triiodothyronine. **2** *abbr. for* bacteriophage T3, a **T-odd phage**.

T4 **1** *or* T_4 *symbol for* L-thyroxine. **2** *abbr. for* bacteriophage T4, a **T-even phage**.

T6 *abbr. for* bacteriophage T6, a **T-even phage**.

T7 *abbr. for* bacteriophage T7, a **T-odd phage**.

tA *symbol for* N^6-(threonylcarbamoyl)adenosine; *see* **hypermodified base**.

Ta *symbol for* tantalum.

tachometer an instrument that measures the speed at which any object is rotating. —**tachometric** *adj.*; **tachometry** *n.*

tachy+ *comb. form* denoting fast or rapid.

tachykinin any of a group of closely related vasoactive peptides characterized by a rapid stimulant effect on vascular (and extravascular) smooth muscle, producing hypotension (*compare* **bradykinin**). They also directly effect nervous tissue and stimulate salivary and lachrymal secretion. Naturally occurring tachykinins are oligopeptide amides containing 10–12 amino-acid residues and terminating in the common sequence -Phe-Xaa-Gly-Leu-Met-NH_2 (where Xaa = Phe, Tyr, Ile, or Val). Mammalian tachykinins include neuromedin K, **neurokinin A** (formerly substance K), and **substance P**; others (e.g. **eledoisin**, **physalaemin**) occur in amphibians and octopods. Substance P and neurokinin A are generated from a preprotachykinin protein precursor (*see* **protachykinin β precursor**). The primary mRNA transcript is differentially processed into three mature mRNAs: α, β, and γ; the β and γ preprotachykinin mRNAs are predominant in the rat, each encoding substance P and neurokinin A. Example, human (precursor): database code TKNB_HUMAN, 129 amino acids (15.00 kDa).

tachykinin receptor any of a number of membrane proteins that bind **tachykinins** and mediate their transmembrane action. They fall according to the relative potency of agonists into three classes: (1) NK_1 (407 amino acids, human), agonist potency: substance P (SP) > neurokinin A (NKA) > neurokinin B (NKB); (2) NK_2 (398 amino acids, human), agonist potency: NKA > NKB >> SP; and (3) NK_3 (452 amino acids, rat), agonist potency: NKB > NKA > SP. All are of the seven-transmembrane-domain type and share significant sequence similarity with G-protein-coupled receptors. The effector pathway in all cases is by activation of phosphoinositide-specific phospholipase C. Example of putative receptor from human: database code TXKR_HUMAN, 440 amino acids (49.43 kDa).

tachyphylaxis a decline in the response to repeated applications of doses of agonists. *See also* **desensitization**, **fade**.

tachyplesin any of a group of arthropodous peptide antibiotics, 17 or 18 amino acids long and with a C-terminal arginine α-amide. They are abundant in acid extracts of hemocyte debris of horseshoe crabs (*Tachypleus* spp.). They strongly inhibit the growth of Gram-positive and Gram-negative bacteria, and of fungi such as *Candida albicans*. Example from *Tachypleus gigas*: database code TAC3_TACGI, 17 amino acids (2.24 kDa).

tac **promoter** a hybrid **promoter**, constructed *in vitro*, that contains the –35 sequence of the *trp* promoter and the –10 sequence of the *lacZ* promoter. *See* **minus 10 region**.

Tacrolimus *see* **FK506**.

tactic polymer a regular polymer in whose molecules there is an ordered structure with respect to the configurations around at least one main-chain site of stereoisomerism per **constitutional base unit**.

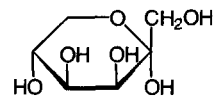
tactile capable of exciting the sense of touch; relating to the sense of touch (as a sense organ).

tactoid a **paracrystal**-like aggregate; the term may be applied to the rodlike filaments of hemoglobin that form in **sickle cells**, or to assemblies of virus particles (e.g. of tobacco mosaic virus).

tag **1** to identify by a marker; for example, a cell may be tagged by attachment of a (fluorescent or radiolabelled) antibody. **2** an identifier used in tagging.

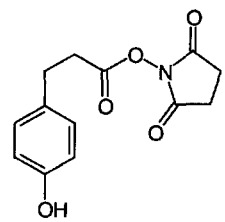
Tagamet *see* **cimetidine**.

D-tagatose *a nonsystematic name for* D-*lyxo*-2-hexulose, a hydrolysis product of some plant gums.



α-D-pyranose form

Tagit *a proprietary name for N*-succinimidyl 3-(4-hydroxyphenyl) propionate; a substance used in the preparation of **Bolton and Hunter reagent** for tagging peptides and proteins with radioiodine.



tail **1** an extension growing or appending from a point of origin

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or attachment. For example, the fatty-acyl groups of a phospholipid and the glycerol to which they are bonded are referred to as the tail. *Compare* **headgroup**. **2** *(in chromatography)* a region of more slowly moving or decomposed material extending back from a band towards the **origin**. *See also* **poly(A) tail**, **tailing**.

tailing **1** the addition of a stretch of identical nucleotides to the ends of a restriction fragment using **terminal deoxynucleotidyl transferase**. **2** the spreading out of a band or spot in a chromatographic process.

Tal *symbol for* a residue, or sometimes a molecule, of **talose**.

talaric acid one of the **hexaric acids**; *see also* **aldaric acid**.

talc a soft mineral composed of hydrated magnesium silicate, $Mg_3Si_4O_{10}(OH)_2$, with small quantities of metal impurities. In its powdered form it is known as talcum powder, or French chalk, and in granular form as soapstone (steatite). Powdered talc is used as a lubricant, as a filler in paper and other products, and in cosmetics, etc.

talcum powder powdered **talc**.

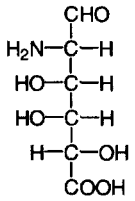
talin a protein involved in connections between the cytoskeleton and the plasma membrane. A phosphoprotein, it binds strongly to **vinculin**, and less strongly to **integrins**. It is a founder member of the **TERM** family. Example from mouse: database code TALI_MOUSE, 2541 amino acids (269.53 kDa).

talo+ *or (before a vowel)* **talos+** *comb. form* of **talose**.

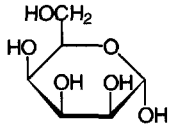
talo- *prefix (in chemical nomenclature)* indicating a particular configuration, a set of (usually four) contiguous CHOH groups as in the acyclic form of D- or L-**talose**. *See also* **monosaccharide**.

talopeptin *N*-(6-deoxy-α-L-talopyranosyl-oxyphospho)-L-leucyl-L-tryptophan; an inhibitor of several metallopeptidases, including **thermolysin**. *Compare* **phosphoramidon**.

talosaminouronic acid a component of the **peptidoglycan** of Archaea.



talose *symbol*: Tal; *the trivial name for* the aldohexose *talo*-hexose, which differs from glucose in the configuration of the groups at C-2 and C-4; there are two enantiomers.

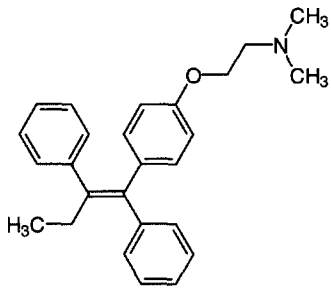


α-D-talose

Tamm, Igor Yevgenyevich (1885–1971), Russian-born Soviet physicist; Nobel Laureate in Physics (1958) jointly with P. A. Cherenkov and I. M. Frank 'for the discovery and the interpretation of the Cherenkov effect'.

Tamm–Horsfall glycoprotein *or* **uromodulin** *the principal* glycoprotein of human urine. It occurs in other species, e.g. the cow and rat. The molecule is filamentous with an M_r of several million and is composed of subunits of $M_r \approx 80\,000$; it contains about 25% carbohydrate and a small amount of lipid. An abnormally high M_r is observed in cystic fibrosis. Example from human (precursor): database code UROM_HUMAN, 640 amino acids (69.76 kDa). *See also* **proteinuria**. [After Igor Tamm (1922–71), US virologist and Frank Lappin Horsfall (1906–71).]

Tamoxifen [*Z*]-2-[4-(1,2-diphenyl-1-butenyl)-phenoxy]-*N*,*N*-dimethylethanolamine; *the proprietary name of* an estrogen antagonist, used in the treatment of breast cancer and suggested for use as a prophylactic drug in women with a family history of breast cancer. The drug has complex pharmacological properties and can behave as a pure estrogen agonist, a partial agonist, or an antagonist, depending on the species of animal, the target organ examined, and the endpoint measured. It is a **genotoxic** carcinogen in the rat.



tan *abbr. for* tangent (def. 1).

tandem-crossed immunoelectrophoresis *see* **crossed immunoelectrophoresis**.

tandem repeat **1** (of DNA sequences) an arrangement in which two or more copies of a particular base sequence are situated immediately one after the other. Tandem repeats are commonly found in **telomeres**, the repeated sequence being characteristic of species and source of DNA, and of relatively short length (up to about 10 bases). They also occur in **highly repetitive DNA**. **2** (of genes) a cluster of adjacent multiple copies of the same gene. The genes for ribosomal RNA (rRNA) are characteristically contained in tandem clusters, sometimes referred to as **ribosomal DNA** (rDNA). *See also* **concatemer**.

Tanford–Kirkwood theory a theory of protein titration curves based on a model in which the charges are taken to be discrete unit charges located at fixed positions on the protein molecule. [After Charles Tanford (1921–) and John Gamble Kirkwood (1907–59).]

tangent **1** *abbr.*: tan; a function of an angle, being, in a right-angled triangle, the ratio of the side opposite the given angle (if acute) to that of the side opposite the other acute angle. The tangent of an obtuse angle is numerically equal to that of its supplement but of opposite sign. **2** a straight line that touches, but does not cut, a curve or a curved surface.

tangential-flow filtration a convenient and rapid method of concentrating cells, cell organelles, or other particulate material, or for eliminating such material from solutions. Using a special apparatus, the suspension containing the material is caused to flow over ('tangential flow') a semipermeable membrane; only material smaller than the membrane pores will pass through the membrane, forming the filtrate, leaving larger matter to be collected (retentate).

Tangier disease a rare autosomal recessive condition in humans in which there is a deficiency or complete absence of **high-density lipoprotein**. Homozygotes have very low levels of **apolipoprotein A-I**. There is accumulation of cholesterol esters in cells of the mononuclear phagocyte system. The condition is relatively benign as organ function is not affected. [After Tangier Island, Chesapeake Bay; the disease was first found in inhabitants of this island.]

tannic acid *or* **tannin** *or* **gallotannin** *or* **gallotannic acid** *an imprecise term used for* a mixture of hydrolysable **tannins** (def. 1).

tannin **1** any of a group of polyphenolic plant products that

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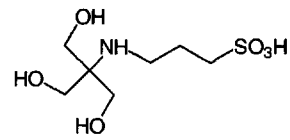
can be used to tan animal skins to produce leather. The term was introduced in 1796. Tannins are divided into **hydrolysable tannins** (the larger group) and **condensed tannins**. The former consist of a core of a polyhydric alcohol, usually glucose, esterified with either gallic acid or hexahydroxydiphenic acid. Condensed tannins are polymers of flavans and never contain sugar residues; they are often termed **flavolans**. Tannins form insoluble protein tannates with proteins, which, when the protein is a skin protein, forms the basis of **tanning** (def. 1). The liberation of tannins during the extraction of plant enzymes can cause difficulties because they tan enzymes, i.e. form insoluble tannates. The addition of polyvinylpyrrolidone may help to avoid this problem. Good tanning agents should have an M_r of between 500 and 3000 and contain sufficient phenolic hydroxyl groups (1–2% of M_r) to form effective cross-links with protein. **2** *a common name for* **tannic acid**.

tanning **1** a technique of considerable antiquity, being known by the Egyptians around 3000 BC, for producing leather from animal skins by the use of **tannin** (def. 1). Modern methods using chrome salts are faster, taking a few hours rather than weeks. **2** the treating of red blood cells with tannic acid. Such cells are used in a test for anti-thyroglobulin antibodies, after they have been treated with thyroglobulin. The tanning enhances sensitivity.

T antigen **1** any of the several early gene products of a genetic locus of certain transforming DNA viruses, including adenovirus, simian virus 40 (SV40), and polyoma virus. The substance originally detected in nuclei of transformed cells by immunofluorescence (hence the name antigen; the 'T' indicates tumour or transformation) led to the identification of several products, the genes of this locus encoding a number of essential early proteins that are needed for replication. Two products are formed by SV40, known as **large T antigen** (*or* T antigen) and **small t antigen** (*or* t antigen). Polyoma virus expresses three products from this locus, large T antigen, middle T antigen, and small t antigen. Large T antigen of SV40 alone is sufficient to immortalize primary rodent cells and transform established rodent cell lines. It is a multifunctional protein that is a potent transcriptional activator which promiscuously activates simple promoters containing a TATA box or initiator element and at least one upstream transcription-factor-binding site. Examples, large T antigen from SV40: database code TALA_SV40, 708 amino acids (81.58 kDa); large T antigen from polyoma virus: database code TALA_POVMK, 648 amino acids (74.71 kDa). Middle T antigen of polyoma virus is essential for polyoma-virus-mediated tumorigenesis and cell transformation. It associates with and activates cellular tyrosine kinases, including c-Src, c-Yes, and Fyn, and also binds phosphatidylinositol 3-kinase and protein phosphatase 2A. Example, middle T antigen of polyoma virus: database code TAMI_POVMA, 442 amino acids (48.62 kDa). Small t antigen of SV40 exercises a helper effect in SV40 transformation. It forms complexes with protein phosphatase 2A and regulates the phosphorylation and transcriptional transactivation of **CREB protein**. It stabilizes p53 in a manner that correlates with enhanced transformation efficiency of SV40. Example, small t antigen from polyoma virus: database code TASM_POVMA, 195 amino acids (22.81 kDa). **2** an antigen found on normal human erythrocytes that is unreactive unless the cells are first treated with neuraminidase. **3** one of the principal protein antigens in the cell wall of *Streptococcus* spp. **4** *abbr. for* transplantation antigen (i.e. a class I MHC antigen); see **major histocompatibility complex**.

tapeworm any parasitic flatworm (phylum Platyhelminthes) belonging to the class Cestoda.

Taps *or* **TAPS** *abbr. for N*-tris(hydroxymethyl)methyl-3-aminopropanesulfonic acid; 3-{[2-hydroxy-1,1-bis(hydroxymethyl)-ethyl]-amino}propanesulfonic acid; a **Good buffer substance**, pK_a (20 °C) = 8.4.



Taps

***Taq* DNA polymerase** a heat-stable DNA polymerase from *Thermus aquaticus*, a thermophilic bacterium. It is used in the **polymerase chain reaction**.

tare **1** to compensate for the weight of a container, etc. when weighing, by adjusting the balance to zero with the empty container in place before adding the material to be weighed. **2** the weight of the tared vessel or material.

target the object at which an action or process is directed. For example, a **target cell** is the cell under attack by a cytolytic or killer cell or other cytolytic agent, and a **target tissue** is the tissue that is acted on by any hormone, growth factor, or other agonist.

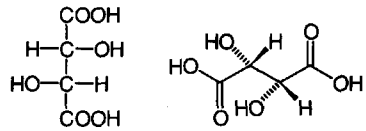
targeting subunits protein subunits that specify the location and catalytic and regulatory properties of protein phosphatases and kinases.

target repeat *see* **transposon**.

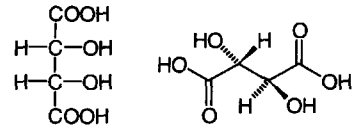
target site the site at which a **restriction endonuclease** cleaves a DNA molecule; usually the same as the **recognition site** (def. 2).

target theory *(in radiation chemistry)* a theory stating that all single hits on biologically active macromolecules by particles or quanta of ionizing radiation result in damaged and inactive molecules, that no partially active molecules are formed, and that all unhit molecules retain full activity.

tartaric acid 2,3-dihydroxybutanedioic acid; 2,3-dihydroxysuccinic acid; one of the **aldaric acids** formed by oxidation of a **tetrose** at C-1 and C-4. The L-(+) (*see* **D/L convention**), or 2*R*,3*R*, enantiomer occurs widely in plants, especially grape juice, and in fungi and bacteria; the D-(–) (or 2*S*,3*S*) enantiomer and *meso* form have limited distribution in plants. The racemic mixture, DL-tartaric acid, sometimes occurs during wine manufacture; it was originally known as **paratartaric acid**. The first determination of an absolute configuration by anomalous dispersion of X-rays was made on sodium rubidium L(+)-tartrate in 1951. The property of **optical activity** of some substances was first described by **Pasteur** in experiments with crystals of sodium ammonium tartrate.



L-form



meso-form

TATA-binding protein *abbr.*: TBP; a component of transcription factor IID (*see* **TFII**). *See also* **RNA polymerase**.

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TATA box *or* **Hogness box** a base-sequence element common in eukaryotic promoters, characterized by the consensus TATAAAA. It binds a general transcription factor and hence specifies the position where **transcription** is initiated.

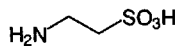
Tatum, Edward Lawrie (1909–75), US microbiologist; Nobel Laureate in Physiology or Medicine (1958) jointly with G. W. Beadle 'for their discovery that genes act by regulating definite chemical events' [prize shared with J. Lederberg].

tau **1** *symbol*: τ (lower case) *or* T (upper case); the nineteenth letter of the Greek alphabet. For uses *see* **Appendix A. 2** *an alternative name for* transcription factor TFIIIC; *see* **TFIII**.

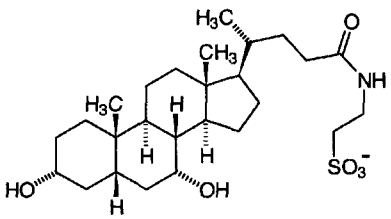
tau protein a microtubule-associated protein that promotes microtubule assembly and stabilizes microtubules. It constitutes at least a part of the paired helical filament (PHF) core found in **Alzheimer's disease**. Example from human: database code TAU1_HUMAN, 383 amino acids (39.96 kDa).

tau-protein kinase EC 2.7.1.135; an enzyme that catalyses the phosphorylation by ATP of τ-protein to *O*-phospho-τ-protein. Example bovine (fragment): database code S43683, 209 amino acids (23.14 kDa). *See also* **tau protein**.

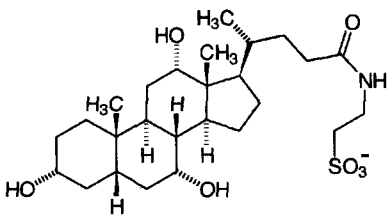
taurine 2-aminoethanesulfonic acid; a compound that is derived metabolically from cysteine by oxidation of the sulfhydryl group to sulfoxide followed by decarboxylation of the resulting cysteic acid. *N*-conjugated with cholic acid, it forms the bile salts **taurochenodeoxycholate**, **taurocholate**, and **taurodeoxycholate**.



taurochenodeoxycholate the anionic form of the amido conjugate of **taurine** and **chenodeoxycholate**. It is a major **bile acid**.



taurocholate the anionic form of taurocholic acid, *N*-cholyltaurine, a major **bile salt** of humans and other mammals. It is useful as an anionic bile-salt detergent (aggregation number 4; CMC 3–11 mM). The anions of similar taurine conjugates of other bile acids are known, e.g. **taurochenodeoxycholate** and **taurodeoxycholate**.



taurocyamine *N*-(aminoiminomethyl) taurine; a compound found in marine polychaete worms. The guanidine group can undergo phosphorylation, to form phosphotaurocyamine, which acts as a **phosphagen**.

taurodeoxycholate the anionic form of taurodeoxycholic acid, *N*-(7-deoxy)cholyltaurine. It is useful as an anionic bile-salt detergent (aggregation number 6; CMC 1–4 mM).

taurolipid any of a class of lipids consisting of a non-hydroxy fatty acid esterified with a hydroxy group of tri-, tetra-, or pentahydroxystearic acid in amide linkage with taurine. They are characteristic lipids of the protozoan *Tetrahymena*.

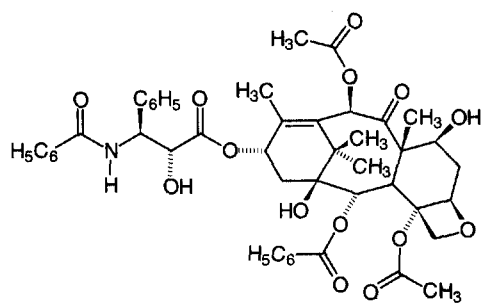
tauryl the acyl group, $H_2N–CH_2–CH_2–SO_2–$, derived from taurine.

taut form *abbr.*: T form; *see* **tense form, Monod–Wyman–Changeux model for allosteric interaction**.

tautomer any one of the possible alternative structures that may exist as a result of **tautomerism**.

tautomerism a form of constitutional isomerism in which a structure may exist in two or more constitutional arrangements, particularly with respect to the position of hydrogens bonded to oxygen. The isomers, or tautomers, are readily interconvertible and exist in equilibrium. The best-known example is **keto–enol tautomerism**, in which the structures X–C(=O)–CH_2–X (keto) and X–C(OH)=CH–X (enol) exist, in proportions determined by the equilibrium position for the conditions pertaining (normally strongly favouring the keto form). Other examples include quinone–quinol and **amino–imino tautomerism**. —**tautomeric** *adj.*

taxol an antitumour and antileukemic agent isolated from the bark of the Pacific yew, *Taxus brevifolia*. It is used clinically to treat refractory ovarian cancer. Its anticancer activity results from its ability to inhibit mitosis and block the cell cycle in its G or M phases through enhancement of the polymerization of **tubulin** and the consequent stabilization of the **microtubules**. In view of the endangered status of *T. brevifolia*, taxol is manufactured semisynthetically from a material present in *T. baccata*. A total chemical synthesis has also been achieved. After the discovery of taxol, a compound with similar properties was isolated from the myxobacterium *Sporangium cellulosum*. This compound, **epothilone**, is more water-soluble than taxol and has the advantage that it can be produced in quantity by fermentation. Taxol and its analogues are known as **taxanes**. One proprietary name is Paclitaxel. A proprietary name of a semisynthetic analogue is Docetaxel.



taxon (*pl.* **taxa**) a named taxonomic group of any rank; a particular taxon comprises organisms having certain genetic characters in common. Strictly, the term should be used to denote only named groups, e.g. Chordata, Hominidae, etc., not as a generic term for the ranks themselves, e.g. phylum, family, etc.

Tay–Sachs disease *or* **G_{M2} gangliosidosis** an inherited neurological metabolic disorder resulting from deficiency of the lysosomal enzyme, **hexosaminidase** (form A, deficiency in α chain). This leads to the accumulation of its substrate, ganglioside G_{M2} (*see* **ganglioside**), in the brain. The disease is relatively common (1 in 2500 live births) among Ashkenazy Jews. There is motor and mental deterioration with an exaggerated startle response to sound; by 18 months of age, most patients are blind, deaf, and spastic; they die by the age of 3 years. *See also* **saposin**. [After Warren Tay (1843–1927), British physician and Bernard Sachs (1858–1944), US neurologist.]

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Tb *symbol for* terbium.

TBP *abbr. for* TATA-binding protein (*see* **TFII, RNA polymerase**).

tBu *abbr. for* tertiary butyl (alternative to Bu^t).

TBW *abbr. for* total body water; *see* **body water**.

Tc *symbol for* technetium.

TCA *abbr. for* **1** tricarboxylic acid. **2** trichloroacetic acid.

TΨC arm the base-paired segment of the clover-leaf model of **transfer RNA** to which the loop containing the base sequence TΨC is attached (Ψ = pseudouridine).

T cell *an alternative name for* **T lymphocyte**.

T_H cell *abbr. for* **helper cell**.

T-cell growth factor *abbr.*: TCGF; *an alternative name for* **interleukin 2**.

T-cell receptor a heterodimer glycoprotein of the immunoglobulin superfamily located in the plasma membrane of T cells (**T lymphocytes**). T-cell receptors have structural similarities with class II MHC antigens (*see* **major histocompatibility complex**) but the α and β chains are disulfide bonded. They are responsible for recognition of target antigen in combination with MHC. After binding to antigen/MHC (class I or class II depending on the type of antigen presentation), the T-cell receptor transduces the signal into the T cell, probably through mediation by associated CD3 molecules (see **CD marker**), and brings about T-cell activation. One constant region and one variable region (*see* **immunoglobulin**) are located in each subunit (α and β); the subunits are related to one another. As with immunoglobulins, the variable regions are designed for specificity of recognition (but they are not products of the immunoglobulin genes). A small number of adult T-cell receptors have γ and δ chains. This class of receptor appears first in ontogeny. Examples from human leukemic cell line, constant regions; α subunit: database code TCA_HUMAN, 142 amino acids (15.91 kDa); β subunit: database code TCB_HUMAN, 177 amino acids (19.88 kDa).

T-cell-replacing factor *abbr.*: TRF; a term formerly used for some interleukins. *See* **interleukin 1, interleukin 5**.

TCGF *abbr. for* T-cell growth factor (i.e. **interleukin 2**).

T chain *an alternative name for* **secretory piece**.

TCP-1 *abbr. for* T-complex protein 1; a **molecular chaperone** that forms two stacked rings, 12–16 nm in diameter and is associated with other proteins in a 850–900 kDa complex. It is similar in function to Hsp60 (a **heat-shock protein**) in mitochondria and the ***groEL*** product in bacteria (*see also* **chaperonin**). Example from human: database code TCP1_HUMAN, 556 amino acids (60.27 kDa).

T-DNA *abbr. for* transfer DNA; that part of the *Agrobacterium* **Ti plasmid** that is incorporated into the genome of infected plant cells. It is approximately 23 kb long and codes for an **opine**, usually **nopaline** or **octopine**, which the transformed cells produce and the bacteria then use. At each end of the T-DNA in the Ti plasmid there is a 25 bp sequence; the right hand one of these almost identical sequences is essential for the transfer process.

TDP *abbr. for* **1** ribosylthymine diphosphate *or* ribothymidine diphosphate, *the common names for* ribosylthymine 5′-diphosphate, ribothymidine 5′-diphosphate, 5′-ribothymidylyl phosphate, thymine riboside 5′-diphosphate. **2** *(sometimes)* thymidine diphosphate (dTDP is recommended).

Tdr *or* **TdR** *or* **TDR** *abbr. for* thymine deoxyriboside (i.e. thymidine). Use deprecated; the symbol dThd is recommended.

TdT *abbr. for* **terminal deoxynucleotidyltransferase**.

Te *symbol for* tellurium.

TEA *abbr. for* **1** triethanolamine; $N(CH_2CH_2OH)_3$; a base used in the preparation of buffers, pK_a (25 °C) 7.90. **2** tetraethylammonium; used to block sympathetic and parasympathetic ganglionic transmission; normally used as the chloride.

TEAE *abbr. for* the triethylaminoethyl group, $(C_2H_5)_3NCH_2CH_2$–. It may be used as a substituent in hydroxylated chromatographic support matrices, e.g. cellulose, Sephadex, to form anion-exchange columns.

teichoate the anionic form of **teichoic acid**.

teichoic acid any polymer occurring in the cell wall, membrane, or capsule of Gram-positive bacteria and containing chains of glycerol phosphate or ribitol phosphate residues. Additionally, carbohydrates are linked to glycerol or ribitol, and some –OH groups are esterified with D-alanine.

tektins a family of similar proteins that are adapted to the assembly of a variety of eukaryotic cell structures. Tektins have common features that adapt them to sensitive and specific associations with molecules of their own kind; they have similar amino-acid compositions. They include actin, actin-like proteins, some microtubule proteins, mitochondrial structural protein, and erythrocyte membrane proteins.

tele a designator of the position of one of the nitrogens of the histidine imidazole ring, indicating the nitrogen furthest from the side chain. It is often symbolized by τ, as in N^{τ}. *Compare* ***pros***.

teleology the doctrine or study of ends or final causes, especially as related to the evidences of design or purpose in nature; the use of design, purpose, or utility as an explanation of any natural phenomenon. An example of a teleological concept in biology is that organs are made to react for the good of the organism as a whole.

teleonomy the idea that the existence of a structure or a function in an organism must have conferred an evolutionary advantage upon that organism.

teleost any member of the infraclass Teleosti, comprising fishes with rayed fins and a swim bladder; it includes most of the extant bony fishes.

telestability the transmission of three-dimensional stability from a stable part of a macromolecule to an inherently less stable part.

telokin the C-terminal sequence of smooth muscle **myosin-light-chain kinase** expressed as an independent protein. It binds calmodulin. Example from rabbit: database code TELO_RABIT, 155 amino acids (17.18 kDa).

telolysosome a **lysosome** that has accumulated so much indigestible residue that it is unable to accumulate further material to be digested. The structure still contains enzymes but these are no longer renewed. *Compare* **residual body**.

telomerase EC 2.7.7.–; a DNA polymerase enzyme involved in **telomere** formation, and in telomere elongation to maintain the telomere sequences during replication. The enzyme recognizes the G-rich strand of an existing telomere repeat sequence, elongating it in the 5′ to 3′ direction. *Tetrahymena* telomerase is a large ribonucleoprotein, a specialized example of a reverse transcriptase. The RNA component includes a template for synthesizing the G-rich repeating sequence. The ***EST1*** gene product is a probable example.

telomere the structure that seals the end of a chromosome. In order to counteract the tendency of the chromosome otherwise to shorten with each round of replication, the telomeric DNA consists of simple tandemly repeated sequences specific for each species. Typically one strand is G-rich and the other C-rich. The G-rich strand forms a 3′-terminal overhang about 15 residues long. These are the sequences added to the 3′ terminus of chromosomal DNAs by **telomerase**. The elongation allows a primer to bind and initiate synthesis on the other strand, maintaining the length of the chromosome and preventing the loss of coding sequences. —**telomeric** *adj.*

telopeptide any of the peptides that protrude from the triple-helical body of **tropocollagen** and have a composition different from the triple-helical portions. They are removed by proteases, with concomitant breakage of intramolecular interchain bonds. They are thought to occupy near-terminal positions. The antigenic response to injected heterologous tropocollagen is directed against these telopeptide appendages external to the triple helix.

telophase the final stage of **mitosis** or **meiosis** in which the nuclei form in the daughter cells, which then revert to the resting state.

TEM *or* **T.E.M.** *abbr. for* **1** transmission electron microscope;

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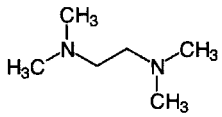
see **electron microscope**. **2** Tris–EDTA–mercaptoethanol (buffer).

TEMED *abbr. for* *N,N,N′,N′*-tetramethylethylenediamine; *N,N,N′,N′*-tetramethyl-1,2-diaminoethane; a substance used as a polymerizing agent in the preparation of polyacrylamide gels. It acts to stabilize free radicals produced by ammonium persulfate.



Temin, Howard Martin (1934–94), *US virologist*; Nobel Laureate in Physiology or Medicine (1975) jointly with D. Baltimore and R. Dulbecco 'for their discoveries concerning the interaction between tumour viruses and the genetic material of the cell'.

temperate phage a **bacteriophage** that, following infection of its host bacterium, may either enter the lytic cycle, like a **virulent phage**, or establish a kind of symbiotic relationship with the host cell that results in its subsequent perpetuation in all the descendants of the bacterium. Bacteria carrying temperate phage are said to be **lysogenic**, while the form of the carried phage is known as a **prophage**.

temperature *abbr.*: temp.; a fundamental physical quantity of a body, region, or system that determines the direction of net heat flow between it and its surroundings. If two systems have the same temperature they are in thermal equilibrium and there is no net heat flow between them. If they have different temperatures they are not in thermal equilibrium and heat flows from the system of higher temperature to that of lower temperature. Essentially there are two different methods of measuring temperature. One is to use a scale of values set up between arbitrary fixed points based on reproducible temperature-dependent events. For example, the **Celsius temperature** scale uses a freezing point and boiling point of water as fixed points, to which are assigned the values 0 and 100, respectively; the scale between them is divided into 100 degrees. Although widely used for many practical purposes, it lacks a theoretical basis and is unsuitable in many scientific contexts. Instead, the concept of **thermodynamic temperature** is used. This is defined in terms of the second law of thermodynamics (*see* **thermodynamics**) and is independent of any particular substance. However, in practice thermodynamic temperatures cannot be measured directly. Consequently, a practical realization of the thermodynamic temperature scale is used, called the **International Practical Temperature Scale** (IPTS). This is based on a number of fixed points, and is measured in **kelvins**; it defines temperature down to 13.81 kelvins, the triple point of equilibrium hydrogen.

temperature coefficient of a reaction *symbol*: Q_{10}; the factor by which the velocity of a chemical reaction is increased by raising the temperature, t, by 10 °C. Usually it is the ratio of the rate of reaction at (t + 10°) to that at t, denoted by $Q_{10} = k_{t+10}/k_t$, where k_{t+10} and k_t are the rate constants at the respective temperatures. The Q_{10} value of homogeneous chemical reactions is generally in the range 2–3; many enzyme-catalysed reactions and physiological processes exhibit, over a limited range of temperatures, a Q_{10} value of ≈2. *See also* **Arrhenius equation**.

temperature jump a technique used in **relaxation kinetics** for the study of enzyme mechanisms in which the temperature is raised rapidly (e.g. over about 1 μs), the reaction being monitored during this and the subsequent (very short) period during which the system relaxes to a new equilibrium.

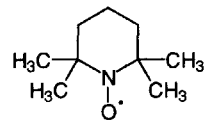
temperature-sensitive mutation a mutation that is manifest in only a limited range of temperature. The mutant carrying such a mutation behaves normally at the lower, **permissive temperature**, but when grown at the lower or higher, **restrictive temperature**, it shows the mutant phenotype.

template a macromolecule whose structure serves as a pattern for the synthesis of another macromolecule. The term applies particularly to a nucleic acid on which another nucleic acid of complementary base sequence is synthesized, as in genetic **transcription**, or in the case of messenger RNA, on which a polypeptide is synthesized (genetic **translation**).

template RNA *an alternative name for* **messenger RNA**.

template strand *see* **noncoding strand**.

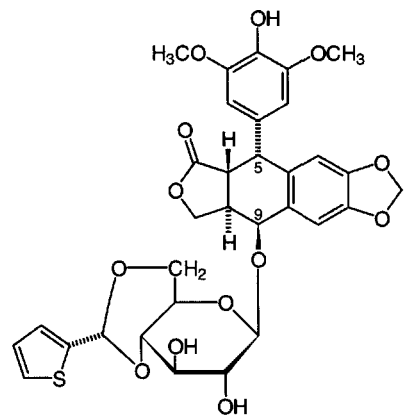
TEMPO *abbr. for* 2,2,6,6-tetramethylpiperidinooxy; 2,2,6,6-tetramethypiperidine 1-oxyl; a stable free radical used as a spin label in electron spin-resonance spectroscopy.



temporal gene any gene that 'programs' a system in time, determining the activation of structural, architectural, and regulatory genes controlling different developmental stages in various cell types.

tenascin a substrate-adhesion molecule of the extracellular matrix that appears to inhibit cell migration and may play a role in supporting the growth of epithelial tumours. It is a hexameric protein; a homotrimer may be formed in the triple coiled-coil region and may be stabilized by disulfide rings at both ends; two such half-hexabrachions (*see* **hexabrachions**) may be disulfide linked within the central globule. Alternative splicing leads to four variants from a single gene in a tissue- and time-specific manner during development. It has EGF-like repeats (*see* **epidermal growth factor**) and **fibronectin** domains. Example from human: database code TENA_HUMAN, 2199 amino acids (240.45 kDa). *Other names*: hexabrachion; cytotactin; neuronectin; gmem; ji; miotendinous antigen; glioma-associated extracellular matrix antigen; gp150–225.

Teniposide a semisynthetic lignan derivative prepared from **podophyllotoxin**. It is similar in action to **Etoposide**, but more potent as a cytotoxic agent *in vitro*.



ten-minute phosphate *see* **labile phosphate**.

tense form *or* **taut form** *abbr.*: T form; the form of an allosteric protein that has a lower affinity for a ligand than the R form (**relaxed form**). *See* **Monod–Wyman–Changeux model (for allosteric interaction)**.

tenside any of the group of surface-active compounds widely

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known as **detergents**. The name derives from their effects on surface tension.

tension 1 the concentration of a gas expressed as the partial pressure of the gas. 2 the force exerted by stretching any material. 3 voltage, electromagnetic force, or potential difference, as in high tension, low tension.

tensor 1 *(in mathematics)* a quantity expressing the ratio in which the length of a **vector** is increased. *Compare* **scalar**. 2 *(in anatomy)* a muscle that stretches or tightens some part while not altering the direction of the part.

tentoxin cyclo[L-leucyl-*N*-methyl-(*Z*)-dehydrophenylalanyl-glycyl-*N*-methyl-L-alanyl]; a cyclic tetrapeptide, originally isolated as a metabolite of *Alternaria alternata*. It selectively induces chlorosis in some plant species when applied to the germinating seedling.

Ter *see* **reactancy of enzymes**.

tera+ *symbol*: T; SI prefix denoting 10^{12} times.

terato+ *or (before a vowel)* **terat+** *comb. form* denoting congenital abnormality.

teratocarcinoma a **teratoma** that includes carcinomatous cells.

teratogen a substance that produces malformations in embryos. —**teratogenic** *adj.*

teratoma a tumour composed of disorganized tissues that are foreign embryologically to the tissue normally found at the site. Teratomas most frequently occur in testis or ovary, and may be derived from remnants of multipotential embryological cells that can differentiate into many cell types.

TERM a family of F-actin binding proteins, named from **talin** and the related proteins **ezrin**, **radixin**, and **moesin**.

terminal amino acid the amino-acid residue at the end of a peptide or polypeptide chain. The **C-terminal amino acid** is the end amino acid that has a free α-carboxyl group (*see* **C terminus**); the **N-terminal amino acid** is the end amino acid that has a free α-amino group (*see* **N terminus**).

terminal deletion *see* **deletion**.

terminal deoxynucleotidyltransferase *abbr.* TdT; EC 2.7.7.31; *recommended name*: DNA nucleotidylexotransferase; *systematic name*: nucleoside-triphosphate:DNA deoxynucleotidylexotransferase; *other names*: terminal addition enzyme; terminal transferase; terminal deoxyribonucleotidyltransferase. An enzyme, commonly isolated from calf thymus, that catalyses the successive transfer of deoxynucleotide residues from the corresponding nucleoside triphosphates to the 3′ end of an oligo- or polydeoxynucleotide. It is a template-independent, Mg^{2+}-dependent **DNA polymerase**. Example (bovine; enzyme used in molecular biology): database code TDT_BOVIN, 520 amino acids (59.60 kDa).

terminal transferase *see* **terminal deoxynucleotidyltransferase**.

terminal web the network of filaments forming the part of the **cytoskeleton** that lies close under the plasma membrane. It is a specialized cortex, to which actin filament bundles may be attached, especially, e.g., at the base of microvilli of intestinal epithelial cells. It contains a dense network of **spectrin** molecules that connect the inner **intermediate filaments** to the actin filaments that are connected to the plasma membrane.

termination codon *or* **terminator codon** any **codon** that signals the termination of a growing polypeptide chain. *See also* **amber codon**, **ochre codon**, **stop codon**.

termination factor any protein that participates in the termination of either transcription (*see* **rho protein**) or translation (*see* **release factor**).

terminator (of transcription) a DNA sequence lying just downstream of the coding segment of a gene that is recognized by RNA polymerase as a signal to stop synthesizing messenger RNA during **transcription**.

termolecular reaction *see* **molecularity**.

ternary consisting of three parts.

ternary complex any complex formed between three chemical entities, e.g. a complex formed between an enzyme and two substrate molecules.

terpene any member of a class of hydrocarbons occurring particularly in most essential oils but represented throughout the biological world. Terpenes are composed essentially of multiples of **isoprene** (C_5H_8) units, and may be acyclic, cyclic, or multicyclic, saturated or unsaturated, and can be substituted by various functional groups, e.g. OH. Terpenes containing 10, 15, 20, 30, 40, or a large number, of carbon atoms per molecule are known as **mono-**, **sesqui-**, **di-**, **tri-**, **tetra-**, or **polyterpenes** respectively. The class is often taken to include alcohol, aldehyde, and carboxylic acid derivatives of terpene hydrocarbons. Isoprene is the only naturally occurring **hemiterpene**, i.e. having five carbons, but the phosphorylated compounds Δ^2- and Δ^3-isopentenyl diphosphates are key intermediates in terpene biosynthesis. *See also* **polyprenyl**.

terpenoid 1 resembling a **terpene** in chemical structure. 2 any member of a class of compounds characterized by an isoprenoid chemical structure (as in a **terpene**) and often including their oxygenated and hydrogenated derivatives.

Terramycin *a proprietary name for* **oxytetracycline**.

tert- *abbr.: t-; prefix (in chemical nomenclature)* signifying **tertiary** (def. 1).

tertiary *(in chemistry)* 1 **a** *prefix*: *tert-* (*abbr.*: *t-*); describing an alkyl compound (e.g. an alkanol) in which the functional group (e.g. a hydroxyl group) is attached to a carbon atom linked to three others. **b** describing the carbon atom bearing the functional group in such a compound. 2 describing an amide or an amine in which three appropriate groups are attached to a nitrogen atom. 3 describing a salt formed by replacing all three of the ionizable hydrogen atoms of a tribasic acid by one, two, or three other cations of appropriate valency. *Compare* **primary**, **secondary**.

tertiary structure the level of protein structure at which an entire polypeptide chain has folded into a three-dimensional structure. The tertiary structure results from interactions between amino-acid residues, that may be widely separated in the primary structure, but may be brought into proximity by the folding of the polypeptide chain. The forces of interaction between residues include hydrogen bonds and electrostatic attraction. The structure is stabilized in some proteins by disulfide bonds. In multichain proteins, the term tertiary structure applies to individual chains. *Compare* **primary structure**, **secondary structure**, **quaternary structure**.

Tes *or* **TES** *abbr. for* *N*-tris(hydroxymethyl)methyl-2-aminoethanesulfonic acid; 2-{[2-hydroxy-1,1-bis(hydroxymethyl)ethyl]amino}ethanesulfonic acid; a **Good buffer substance**; pK_a (20 °C) = 7.5.

tesla *symbol*: T; the SI derived unit of **magnetic flux density**. It is equal to one weber of magnetic flux per square metre; i.e. 1 T = 1 Wb m^{-2}. [After Nikola Tesla (1856–1943), Croatian-born US physicist.]

testicular of, or relating to, the **testis**.

testicular feminization *or* **testicular feminisation** an inherited X-linked condition in which genetic males have developmental abnormalities ranging from a complete external female phenotype to partially masculinized ambiguous genitalia. The primary defect is an unresponsiveness to **dihydrotestosterone**; defects in an X-linked gene coding for a dihydrotestosterone receptor may be responsible.

testis (*pl.* **testes**) the male gonad; in vertebrates there is typically a pair of testes, producing spermatozoa and synthesizing **androgens**.

testosterone 4-androsten-17β-ol-3-one; the principal and most potent androgen. It is formed from androstenedione by 3α(17β)-hydroxysteroid dehydrogenase (NAD^+) (EC 1.1.1.239), in Leydig cells of the testis. Testosterone is responsible during embryonic development for virilization, and promotes and maintains male secondary sex characteristics throughout life. It is also synthesized in the ovary from which some is secreted into the blood, but most is converted to estradiol. Its actions are in large part mediated by **dihydrotesto-**

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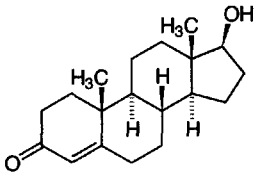
sterone, to which it is converted in target cells. *See also* **androgen receptor**.



tetanus **1** a disease resulting from infection with the bacterium *Clostridium tetani*. *See also* **tetanus toxin**. **2** *or* **tetany** a sustained contraction of a muscle. —**tetanal** *or* **tetanoid** *adj.*

tetanus toxin the protein toxin of *Clostridium tetani*, the causative agent of tetanus. It is a heterodimer of light and heavy chains. It blocks neural exocytosis and thus norepinephrine release, possibly as a result of a Zn^{2+}-dependent proteolysis of **synaptobrevin** by the light chain, but also by inhibition of a neuronal transglutaminase (protein–glutamine γ-glutamyltransferase, EC 2.3.2.13). The protein is synthesized as a precursor: database code TETX_CLOTE, 1314 amino acids (150.55 kDa); this is cleaved to yield the light chain (residues 1–456) and heavy chain (residues 457–1314).

tetanus toxoid the **toxoid** prepared from *Clostridium tetani* toxin and included in anti-tetanus immunogens.

tetany *an alternative term for* **tetanus** (def. 2).

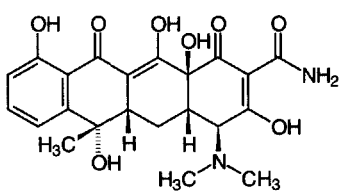
tetra+ *or (before a vowel)* **tetr+** *comb. form* **1** denoting four, fourfold, every fourth; *see also* **tetrakis+** (def. 1). **2** *(in chemical nomenclature)* (*distinguish from* **tetrakis+** (def. 2)) **a** indicating the presence in a molecular entity of four identical specified unsubstituted groups; e.g. tetrachloroethylene, tetramethylammonium chloride. **b** indicating the presence in a molecular entity of four identical inorganic oxoacid residues in linear anhydride linkage; e.g. sodium tetraborate.

tetracosa+ *or (before a vowel)* **tetracos+** *comb. form* indicating twenty-four.

tetracosactide *or* **tetracosactrin** *or* **cosyntropin** *generic names for* β^{1-24}-corticotropin, a synthetic polypeptide identical to the N-terminal 24 residues of of **corticotropin**, and having all of its hormonal activity. It is sometimes known as 1–24 ACTH. Proprietary names include Synacthen.

tetracosapeptide a 24-residue peptide.

tetracycline **1** any of a group of broad-spectrum antibiotics which are also effective against rickettsial organisms, mycoplasmas, and certain protozoa. The bacteriostatic activity of the tetracyclines depends on their direct inhibition of protein synthesis. They are active against protein synthesis on both bacterial 70S and eukaryotic 80S ribosomes although 70S ribosomes are rather more sensitive. The tetracyclines are much more effective against protein synthesis in intact bacteria than against that in eukaryotic cells because of selective absorption by bacterial cells. The tetracyclines inhibit the binding of aminoacyl-tRNA to the acceptor site on the ribosome. **2** any of a group of antibiotics based on the tetracycline nucleus. They include aureomycin (7-chlortetracycline); terramycin (5-oxytetracycline); declomycin (6-demethyl-7-chlorotetracycline); doxycycline (6-deoxy-5-oxytetracycline). *See also* **tetracycline resistant**.



tetracycline resistant *abbr.*: TC^r; resistant to the effects of the antibiotic **tetracycline**. The most commonly encountered mode of resistance depends on a diminished cellular accumulation of these compounds. In enteric bacteria two **transposons**, Tn1721 and Tn10, commonly carry the genes for tetracycline resistance. Tn10 encodes two proteins: a membrane-located protein (M_r 36 000) that appears to mediate resistance and a repressor protein associated with the inducibility of tetracycline resistance. In Gram-positive bacteria the induction mechanism does not appear to involve a repressor protein but depends upon a translational attenuation mechanism. The membrane protein is responsible for a pump that specifically pumps the tetracycline out of the cells against a concentration gradient. Foreign DNA may be fused to the tetracycline-resistance gene in a cloning vector thereby enabling bacterial clones containing the foreign DNA to be selected from those lacking resistance to the antibiotic. The plasmid pBR322 contains genes for resistance to both tetracycline and ampicillin. Insertion of a foreign DNA at certain sites inactivates either or both genes.

tetracycline sensitive *abbr.*: TC^s; sensitive to the effects of **tetracycline**.

tetradeca+ *or (before a vowel)* **tetradec+** *comb. form* indicating fourteen.

tetradecadienoic acid any 14-carbon straight-chain fatty acid having two double bonds. Tetradeca-3*E*,5*Z*-dienoic acid (**megatomic acid**) and the (3*Z*,5*Z*)-isomer are sex attractants for *Attagenus megatoma* and for *A. elongatulus* respectively.

tetradecapeptide a 14-residue peptide.

tetradecenoic acid any 14-carbon monounsaturated fatty acid. Tetradec-9*Z*-enoic acid (**myristoleic acid**) is the most common naturally occurring form, but the 4*Z*-isomer occurs in tohaku oil and the 5*Z*-isomer (**physeteric acid**) in sperm-whale oil.

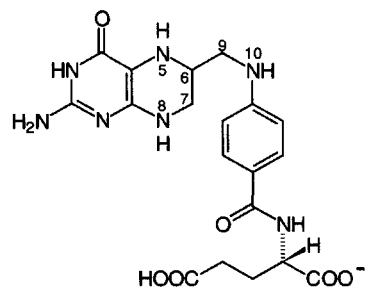
tetraenoic describing an acid having four double bonds. In long-chain fatty acids of the *n*-6 or *n*-3 families (*see* **fatty acid**), these will be **methylene-interrupted double bonds**.

tetragonal symmetry an arrangement, e.g. of a crystal or of ligands around a metal ion in solution, having a single fourfold axis of **symmetry**.

tetrahydro+ *comb. form (in chemical nomenclature)* indicating the presence of four hydrogen atoms at positions of specific interest (in relation to the parent compound, or as specified by a locant).

tetrahydrobiopterin *see* **biopterin**.

tetrahydrofolate *abbr.*: H_4folate *or* (not recommended) THF; *N*-[4-{[(2-amino-3,4,5,6,7,8-hexahydro-4-oxo-pteridin-6-yl)-methyl]amino}benzoyl]-L-glutamate; folate bearing additional hydrogens at positions 5, 6, 7, and 8 of the pterin moiety. It is formed as the reduction product of the action of **dihydrofolate reductase** on dihydrofolate with NADPH as co-substrate.



tetrahydrofuran *abbr.*: THF; tetramethene oxide; an organic solvent that is useful for bringing into aqueous solution com-

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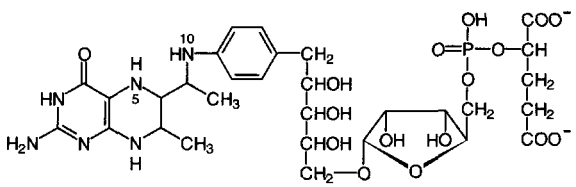
pounds that are otherwise sparingly soluble in water. It is a cyclic ether that is moderately soluble in water.

tetrahydromethanopterin *abbr.*: H_4MPT; a derivative of 7-methylpterin (2-amino-4-hydroxy-7-methylpteridine) that participates in the pathway of methane formation in **methanogenic** bacteria. It undergoes a series of interconversions involving N^5 and N^{10}, analogous to those of the **folate coenzymes**, with formation of formyl-H_4MPT, methenyl-H_4MPT, methylene-H_4MPT, and methyl-H_4MPT.



Tetrahymena a genus of ciliated protozoans, members of which are used in studies of ciliary axonemes, self-splicing RNA, and telomere reproduction.

tetrakis+ *prefix* **1** denoting four times, quadrupled; *see also* **tetra+** (def. 1). **2** *(in chemical nomenclature)* (*distinguish from* **tetra+** (def. 2)) **a** indicating the presence in a molecular entity of four identical specified groups each substituted in the same way; e.g. tetrakis(2-hydroxyethyl)ammonium chloride. **b** indicating the presence at separate positions in a molecular entity of four identical inorganic oxoacid residues; e.g. inositol 1,3,4,5-tetrakisphosphate.

tetrakisphosphate any compound containing four independent phosphoric residues in ester linkages, at positions indicated by locants; e.g. inositol 1,3,4,5-tetrakisphosphate.

tetramer a molecular complex having four components or subunits. If the subunits are identical, the term **homotetramer** is used; if any one is different from any other, the complex is called a **heterotetramer**.

tetraose tetrasaccharide; used as a stem name for any oligosaccharide consisting of four residues per molecule of the same sugar in a single type of linkage, as in cellotetraose. *Distinguish from* **+tetraose** and **tetrose**.

+tetraose *suffix* used in nomenclature of glycolipids to indicate a molecule containing an oligosaccharide moiety composed of four sugar residues (which may be the same or different), as in gangliotetraose. *Distinguish from* **tetraose**.

tetrapeptide a four-residue peptide.

tetraplex DNA *or* **quadruplex DNA** a four-stranded DNA structure adopted by sequences rich in guanine bases. At least two major classes of such structures are known. The first involves the folding back of a repetitive sequence of guanines resulting in antiparallel strands. The other is characterized by the association of four independent parallel strands. *See also* **triplex DNA**.

tetrapyrrole a structure found in **heme** and other **porphyrins**, **chlorophylls**, **bacteriochlorophylls**, **phytochromes**, **phycobilins**, and **corrinoids** (e.g. vitamin B_{12}). It consists of four pyrroles variously substituted and linked to each other through carbons at the α position; in the case of hemes, these links are formed by one-carbon units (methylidene group). Characteristically, a metal is found coordinated to the pyrrole nitrogens, including iron (in hemes), magnesium (in chlorophylls), copper (in **turacin**, the pigment of turaco bird feathers), and nickel (in **factor F_{430}**, a prosthetic group in methanogenic bacteria). Synthesis is via aminolevulinic acid, which is synthesized from glycine and succinyl-CoA in animals and nonphotosynthetic organisms by 5-aminolevulinate synthase. For further steps in the pathway, *see* **porphobilinogen synthase**, **hydroxymethylbilane synthase**, **uroporphyrinogen-III synthase**, and **uroporphyrinogen decarboxylase**.

tetraric acid an **aldaric acid** derived by oxidation of a **tetrose** at C-1 and C-4. There are three tetraric acids, D-, L-, and *meso*-**tartaric acids**.

tetrasaccharide an oligosaccharide with four **monosaccharide** units.

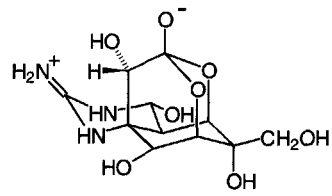
tetrasomic describing any polysomic cell, tissue, or individual in which one chromosome is represented four times in an otherwise **diploid** chromosome complement. *Compare* **monosomic**, **nullisomic**, **trisomic**. —**tetrasomy** *n.*

tetratricosapeptide repeat *abbr.*: TPR; a degenerate consensus sequence of 34 amino acids found in multiple copies in several fungal and other proteins. These sequences participate in RNA synthesis regulation, protein import, and *Drosophila* development. Each sequence has two regions that are stereochemically complementary in α-helical conformation and form a hole and a knob surrounded by hydrophobic residues.

tetrazolium salt any of a group of compounds that are readily reduced to highly coloured, sparingly soluble formazan compounds, and are employed in the assay of some dehydrogenases. They include Blue Tetrazolium and Nitroblue Tetrazolium. **1*H*-tetrazole** is used in the chemical synthesis of oligonucleotides.

tetritol any alditol having a chain of four carbon atoms in the molecule.

tetrodotoxin *abbr.*: TTX; *also known as* **fugu toxin**; a toxin found in the liver and ovaries of the fugu, or puffer fish (order Tetraodontiformes, from which the toxin derives its name). It is a specific, reversible blocker of voltage-gated sodium channels. The LD_{50} in mice is 8 μg kg^{-1}. It does not block potassium or chloride channels.



tetrose any aldose having a chain of four carbon atoms in the molecule. *Distinguish from* **tetraose**.

tetrulose any ketose having a chain of four carbon atoms in the molecule.

T-even phage any one of the **bacteriophages** T2, T4, or T6 of *Escherichia coli*. These DNA phages share a number of morphological, biochemical, and other features that distinguish them as a group from **T-odd phages** and are important historically in research on phages.

Texas Red a red-emitting fluorophore that is a sulfonyl chloride derivative of Sulforhodamine 101. It may be used with **FITC** in dual-label flow microfluorimetric and fluorescent microscopic studies because its excitation and emission spectra do not overlap with those of fluorescein.

TF *abbr. for* **1** tissue factor. **2** transcription factor.

TFII any of a group of **transcription factors** for eukaryotic RNA polymerase II promoters. **TFIIA** is needed for TFIID binding. Example from yeast, a heterodimer comprising large and small chains; large chain: database code TOA1_YEAST, 286 amino acids (32.17 kDa); small chain: database code TOA2_YEAST,

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122 amino acids (13.46 kDa). **TFIIB** binds to RNA polymerase. Example from human: database code TF2B_HUMAN, 316 amino acids (34.79 kDa). **TFIID** has two components, a TATA-binding protein that binds to the **TATA box**, and one of a number of accessory factors; it shows weak homology with bacterial **sigma factors**. Example from human: database code TF2D_HUMAN, 339 amino acids (37.65 kDa). **TFIIE** binds to RNA polymerase; it also shows weak homology with bacterial sigma factors. Example from human, a tetramer of two alpha chains and two beta chains; alpha chain: database code T2EA_HUMAN, 439 amino acids (49.42 kDa); beta chain: database code T2EB_HUMAN, 291 amino acids (33.01 kDa).

TFIII any of a group of **transcription factors** for eukaryotic RNA polymerase III promoters. The examples are all from yeast. **TFIIIA** is a zinc-finger protein (*see* **zinc finger**) that binds both DNA and the 5S RNA transcript; database code S20050, 429 amino acids (49.97 kDa). **TFIIIB** is an RNA polymerase-binding protein. 70 kDa subunit: database code TF3B_YEAST, 596 amino acids (66.83 kDa). **TFIIIC** (*or* **tau**) is a heterotrimer, subunit database codes: TFC1_YEAST, 649 amino acids (73.47 kDa); TFC3_YEAST, 1160 amino acids (131.96 kDa); TFC4_YEAST, 1025 amino acids (120.09 kDa).

TFA *abbr. for* trifluoroacetic acid.

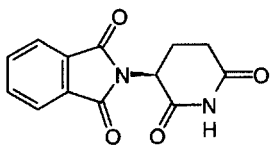
T form *abbr. for* tense form (*or* taut form).

TGF *abbr. for* transforming growth factor.

Th *symbol for* thorium.

thalassemia *or (esp. Brit)* **thalassaemia** any of a group of diseases resulting from inherited defects in the rate of synthesis of one of the types of polypeptide chain of **hemoglobin**. Such defects lead in turn to ineffective erythropoiesis, hemolysis, and a variable degree of anemia. In **alpha thalassemia** the defect is in the production of alpha chains and there is concomitant excessive beta- and gamma-chain production leading to the formation of various abnormal hemoglobins. In **beta thalassaemia** the formation of beta chains is defective with an excessive synthesis of alpha chains and the continued production of fetal hemoglobin ($\alpha_2\gamma_2$).

thalidomide *N*-(2,6-dioxo-3-piperidyl)phthalimide; α-phthalimidoglutarimide; a synthetic tranquillizer and sedative. It was used originally (in the 1950s) as a racemate, which causes severe fetal abnormalities such as the absence or reduction in lengths of one or more limbs. The L(*S*) enantiomer apparently has the teratogenic activity (*see* **teratogen**), while the D(*R*) enantiomer has the desired sedative property. The situation is unclear since thalidomide racemizes rapidly *in vivo*.

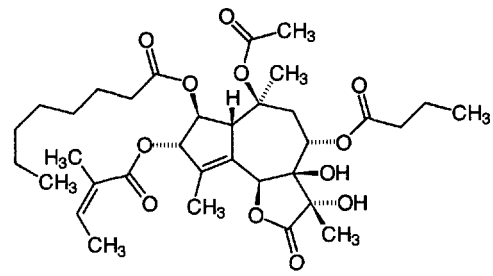


(*S*)-form

THAM *abbr. for* tris(hydroxymethyl)aminomethane; *see* **Tris**.

thanatogene a hypothetical gene whose expression is supposed to lead to cell death in terminally differentiated cells. [From Greek *thanatos*, death.]

thapsigargin a tumour-promoting sesquiterpene lactone. It inhibits endoplasmic reticulum **calcium-transporting ATPase** and mobilizes intracellular calcium.



thapsigargin

thaumatin a sweet-tasting, basic, 20 kDa protein isolated from the berries of the bushy African plant, *Thaumatococcus danielli*; there are five different forms. Its sweetness in aqueous solution is 2500 times greater than that of sucrose; it has sequence similarities with **monellin**.

Thd *symbol for* a residue of the ribonucleoside ribothymidine; ribosylthymine; thymine riboside (alternative to T). *Compare* **dThd**.

Thd5′*P* *symbol for* ribothymidine 5′-phosphate.

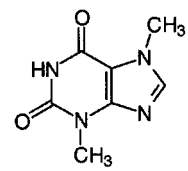
Thd5′*PP* *symbol for* ribothymidine 5′-diphosphate (alternative to ppT).

Thd5′*PPP* *symbol for* ribothymidine 5′-triphosphate (alternative to pppT).

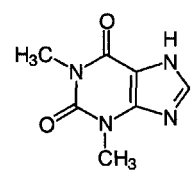
thebaine one of the alkaloids present in opium.

T-helper cell *see* **helper cell**.

theobromine 3,7-dimethylxanthine; the principal alkaloid of the cacao bean. Its actions are similar to those of **theophylline**. *See also* **caffeine**.



theophylline 1,3-dimethylxanthine; a competitive inhibitor of cyclic AMP phosphodiesterase (a 10 mM solution completely inhibits the beef heart enzyme). It has diuretic and cardiac stimulatory action, and relaxes smooth muscle; it is a bronchodilator. *See also* **caffeine**, **theobromine**.



Theorell, Axel Hugo Theodor (1903–82), Swedish biochemist; Nobel Laureate in Physiology or Medicine (1955) 'for his discoveries concerning the nature and mode of action of oxidation enzymes'. *See also* **Theorell-Chance mechanism**.

Theorell–Chance mechanism *(in enzyme kinetics)* an enzyme mechanism in which it is obligatory for substrates to bind in a certain order and in which no kinetically significant ternary complex is formed. [After A. H. T. **Theorell** and Britton Chance (1913–), US biochemist.]

theoretical plate a term used in the analysis of chromatography column performance; the higher the number of theor-

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etical plates achieved, the greater the efficiency of the column. The number of theoretical plates is derived by dividing the peak width by the retention time. The term derives from the concept that the column can notionally be divided into a large number of 'slices' or 'plates' at each of which the separation process will progress. *See also* **effective theoretical plate number**.

therm+ *a variant form of* **thermo+** (before a vowel).

thermal analysis *see* **differential thermal analysis**, **differential scanning calorimetry**.

thermal conductance *symbol*: G; the ability of a material to conduct heat, measured as the ratio of the heat flow rate, Φ, to the temperature difference, i.e. $G = \Phi/\Delta T$. SI units are watts per kelvin.

thermal conductivity *symbol*: λ *or* k; a measure of the ability of a material to transmit heat. It is the heat flux in W m^{-2} divided by the temperature gradient; i.e. $\lambda = J_q/(dT/dl)$, where J_q is the heat flux and dT is the thermodynamic temperature difference over the length, dl. It is measured in watts per metre per kelvin.

thermal denaturation profile a curve relating some physical property of a biopolymer in solution (e.g. viscosity, optical absorbance, or optical rotation) to temperature. The shape of the curve indicates the occurrence of physical changes in the biopolymer, e.g. separation of the two strands of double-stranded nucleic acid or alteration in the tertiary structure of a protein. *See also* **denaturation**, **melting temperature**.

thermal equilibrium the condition of a system when there is no tendency for heat to flow within it, or to or from its surroundings; all parts of the system and its surroundings are at the same temperature.

thermistor a semiconductor whose resistance is sensitive to temperature. [From thermal resistor.]

thermitase EC 3.4.21.66; *other name*: thermophilic *Streptomyces* serine protease; an enzyme that catalyses the hydrolysis of proteins, including collagen. It is a Ca^{2+}-binding serine proteinase from *Thermoactinomyces vulgaris*, and is a homologue of **subtilisin**. It is inhibited by *p*-mercuribenzoate, which reacts with the single cysteine residue near the active-site histidine. Database code THET_THEVU, 279 amino acids (28.33 kDa); 3-D structure known.

thermo+ *or (before a vowel)* **therm+** *comb. form* indicating a relationship to heat or heat transference.

thermobarometer a control manometer and flask used in a **Warburg apparatus**, or other constant-volume-type respirometer, to compensate for changes in temperature and barometric pressure during the course of an experiment.

thermochromism any reversible change of colour of a substance with change of temperature. *Compare* **electrochromism**, **photochromism**. —**thermochromic** *adj.*

thermocouple a device consisting of two pieces of dissimilar metals joined together at a point, their free ends being connected to an instrument to measure electromotive force (emf). The emf produced at the metal–metal junction is a function of the junction temperature, hence a thermocouple may be used to measure temperature. The phenomenon is known as the **Seebeck effect**.

thermodynamicase *(sometimes) an alternative name for* **protein disulfide isomerase**.

thermodynamic equilibrium constant *see* **equilibrium constant**.

thermodynamics the study of the laws that govern the conversion of energy from one form to another, the direction in which heat will flow from one system to another, and the availability of energy to do work. The **zeroth law of thermodynamics** states that if two systems are each in thermal equilibrium with a third system, then they must be in thermal equilibrium with each other. The **first law of thermodynamics** or the **law of conservation of energy** specifies that in an isolated, adiabatic system the sum of the internal energies of all kinds, U, remains constant, whatever may be the changes within the system itself. If a system of constant mass gains heat, q, and has work, w, done on it then a change in its internal energy, ΔU, occurs such that $\Delta U = q + w$. (Where the system loses heat, $q < 0$, and where work is done by it, $w < 0$.) The **second law of thermodynamics** is concerned with the restrictions in the direction of energy flow in natural systems and takes account of the irreversibility of natural processes. It specifies that the entropy of any system, S, unlike energy, is not conserved but increases with time in any spontaneous process in an isolated system. In the limiting case of a reversible process, the increase in entropy of a system, dS, is defined as the heat absorbed by the system, dq_{rev}, divided by the thermodynamic temperature, T; i.e. $dS = dq_{rev}/T$. The **third law of thermodynamics** is concerned with the fact that the difference between the change in enthalpy, ΔH, and the change in the free energy, ΔG, of a system diminishes as the temperature of the system diminishes, and the value of $(\Delta H - \Delta G)$ tends to zero as the thermodynamic temperature tends to zero. This requires that the change in the heat capacity of the system (at constant pressure), ΔC_p, and ΔS must fall to zero at 0 K.

thermodynamic temperature *or (formerly)* **absolute temperature** *symbol*: T; a fundamental physical quantity – one of the seven SI base quantities – defined in terms of the laws of thermodynamics, independently of any particular substance. The SI unit is the **kelvin**. *See also* **temperature**.

thermogenesis the generation of heat by specialized tissues in mammals and in flowers or inflorescences of plants, e.g. arum lilies (*Arum maculatum*). In mammals, this function is performed by **brown adipose tissue**. —**thermogenic** *adj.*

thermogenin *another name for* **brown fat uncoupling protein**.

thermolabile unstable at elevated temperatures. *Compare* **thermostable**. —**thermolability** *n.*

thermolysin EC 3.4.24.27; *other name*: *Bacillus thermoproteolyticus* neutral proteinase; a notably heat-stable, zinc-containing metalloendoproteinase produced by *B. thermoproteolyticus*; it also contains four bound calcium ions. It catalyses the preferential cleavage: Xaa-|-Leu > Xaa-|-Phe. Thermolysin is typical of several such bacterial enzymes: database code NRL_3TLN, 316 amino acids (34.30 kDa); 3-D structure is known.

thermolysis the uncatalysed cleavage of one or more covalent bonds caused by exposing a chemical compound to a raised temperature. *See also* **pyrolysis**. —**thermolytic** *adj.*

thermometer any instrument for measuring temperature. All thermometers depend on the change with temperature of some easily measured physical property such as the expansion of mercury (or other liquids) or the change in electrical resistance. *See also* **thermocouple**.

thermometry the branch of physics concerned with thermometers and the measurement of temperature.

thermoneutron activation analysis *an alternative name for* **radioactivation analysis**.

thermoosmosis the flow of solvent, especially water, across a membrane as a result of a temperature gradient across the membrane.

thermophile an organism, especially a microorganism, that can tolerate high temperatues and that grows optimally at temperatures above 45 °C. *Compare* **mesophile**, **psychrophile**. —**thermophilic** *adj.*

thermoregulator any device or mechanism (including physiological) that controls the temperature of an environment. —**thermoregulatory** *adj.*

thermospray *or* **electron spray mass spectrometer** (*abbr.*: ESMS); an instrument that directly applies a proportion of the eluent of a liquid chromatograph to a mass spectrometer for analysis of resolved components.

thermostable maintaining characteristics or function under a change (normally increased) of temperature. *Compare* **thermolabile**. —**thermostability** *adj. Compare* **thermolabile**.

thermostat 1 an automatic device for regulating temperature, especially maintaining a constant temperature. Such devices often work by cutting off the supply of heat when the required

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temperature is exceeded and restoring it when the temperature falls below the required value. **2** to provide with or to control using a thermostat. —**thermostatic** *adj.*

thermotitration the determination of the endpoint of a reaction, or the point at which the reaction reaches equilibrium, by measurement of heat of reaction.

THESIT *an alternative name for* $C_{12}E_9$ (*see* **C_xE_y**), or Lubrol PX (*see* **Lubrol**).

theta *symbol*: θ (lower case) *or* Θ (upper case); the eighth letter of the Greek alphabet. For uses *see* **Appendix A**.

theta structure the structure that forms during replication of circular duplex DNA by the opening up of the two strands. Under electron microscopy it has the appearance of a Greek theta.

L-thevetose 6-deoxy-4-*O*-methyl-L-glucose; a component of some cardiac glycosides.

THF *abbr. for* **1** tetrahydrofuran. **2** tetrahydrofolate (often used but not encouraged; H_4folate preferred).

thia+ *or (before a vowel)* **thi+** *comb. form* containing sulfur, especially in place of carbon. *See also* **thio+**.

thiamine *or (sometimes)* **thiamin** *or (formerly)* **aneurin(e)** *an alternative name for* **vitamin B_1**.

thiamine diphosphate *or (sometimes)* **thiamin diphosphate** *or (formerly)* **thiamin pyrophosphate** *abbr.*: TPP; *see* **vitamin B_1**.

thick filament a longitudinal assembly of **myosin** molecules occurring in muscle. The thick filaments are the major constituents of the A band of the **sarcomere** in skeletal muscle; they interact with the **thin filaments** to bring about muscle contraction (*see* **sliding filament model**).

thin filament a molecular complex of **actin**, **troponin** (composed of the three peptides troponins I, T, and C), and **tropomyosin**, found in muscle tissue. In striated muscle the thin filaments span the I band and interdigitate between the ends of the **thick filaments** in the A band. Interaction between the thin and thick filaments brings about muscle contraction (*see* **sliding filament model**).

thin-film dialysis a type of **dialysis** that maintains the **diffusate** and the **retentate** in thin layers in intimate contact with the dialysis membrane in order to lessen the contribution to the overall rate of the process made by diffusion of solutes in free solution. Very rapid removal or exchange of small molecules can occur, especially if the volume ratio of diffusate to retentate is high. With appropriate membranes the technique may also be used for analytical studies of the size and conformation of peptides and proteins in solution.

thin-layer chromatography *abbr.*: TLC; chromatography on a thin layer of any of various powdered materials, including silicic acid, aluminium oxide, or cellulose. The layer, characteristically between 0.05 and 1 mm thick, is made to adhere to a sheet of glass, aluminium, or plastic. Thicker layers accept heavier loading, while thinner layers resolve more efficiently and rapidly. Resolving power is high, runs are rapid, and, because support materials such as silicic acid or aluminium oxide are inert to them, corrosive sprays, such as sulfuric acid, can be used to convert organic materials to carbon (a process known as charring), revealing them as black spots.

thio+ *or (sometimes before a vowel)* **thi+** *comb. form* **1** relating to or containing sulfur. **2** *(in chemical nomenclature)* denoting replacement of oxygen in a compound by (bivalent) sulfur. In trivial names of compounds it is used as a prefix (as in thiouracil; *compare* **uracil**), whereas in the systematic names of individual compounds it is used as an affix and is usually placed before the affix denoting an oxygen atom or an oxygen-containing group (as in ethanethiol; *compare* **ethanol**), although for organic sulfides, if named analogously to ethers by substitutive nomenclature, it replaces oxy+ (as in 3-(methylthio)propionate. *Compare* **thia+**. *See also* **mercapto+**.

thioacetal *see* **acetal**.

thioctic acid *a less common name for* **lipoic acid**.

thiocyanate **1** the anion, $N{\equiv}C{-}S^-$, derived from thiocyanic acid. **2** any salt of thiocyanic acid. **3** any organic compound containing the monovalent group –S–C≡N. *Compare* **isothiocyanate**.

thioester any organic compound formed, actually or formally, by the elimination of the elements of water either (1) between the carboxyl group of a carboxylic acid and a thiol, or (2) between the thiocarboxyl group of a thiocarboxylic acid and an alcohol or phenol. Thioesters formed by mechanism (1) are of general formula $R^1{-}CO{-}SR^2$, whereas those formed by mechanism (2) may be of general formula either $R^1{-}CO{-}SR^2$ or $R^1{-}CS{-}OR^2$.

thioether *an old name for* any organic sulfur-containing compound of general formula $R^1{-}S{-}R^2$. Sulfide is now the recommended generic name.

thiogalactoside transacetylase *see* **galactoside acetyltransferase**.

thioglucosidase EC 3.2.3.1; *systematic name*: thioglucoside glucohydrolase; *other name*: sinigrase. An enzyme that hydrolyses thioglucosides to the constituent thiol and sugar, e.g. sinigrin to glucose and *N*-(sulfoxy)-3-mercapto-3-butenimidate.

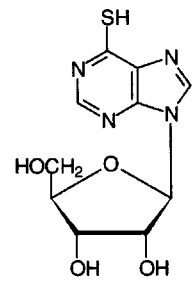
thioglycoside *or* ***S*-glycoside** any glycoside in which a glycosyl group is substituted into a thiol group in another compound. A naturally occurring example is **sinigrin**.

thiohemiacetal *see* **acetal**.

thiohemiketal *see* **acetal**.

thiohypoxanthine *an alternative name for* **mercaptopurine**.

thioinosine *symbol*: sI *or* Sno; 6-thioinosine; thiohypoxanthine riboside; mercaptopurine ribonucleoside; 9-β-D-ribofuranosyl-6-mercaptopurine; a nucleoside not occurring naturally. *See also* **mercaptopurine**.



thioketal *see* **acetal**.

thiokinase *(sometimes)* any of certain ATP-requiring enzymes of sub-subclass EC 6.2.1 (acid thiol ligases) that synthesize CoA thioesters of various fatty acids. These enzymes (recommended names given first) are: (1) **acetate–CoA ligase**, which acts on acetate, propanoate, and propenoate; (2) **butyrate–CoA ligase**; EC 6.2.1.2; *other names*: fatty acid thiokinase (medium chain); butyryl-CoA synthetase; butanoate–CoA ligase (AMP forming); this acts on C_4 to C_{11} acids and on corresponding 3-hydroxy- and 2,3- or 3,4-unsaturated acids; (3) **long-chain-fatty-acid–CoA ligase**; EC 6.2.1.3; *other names*: fatty acid thiokinase (long chain); acyl-CoA synthetase; acid:CoA ligase (AMP forming); this acts on a wide range of long-chain saturated fatty acids, the exact range of chain lengths varying somewhat according to the tissue of origin of the enzyme; and (4) **acetate–CoA ligase (ADP-forming)**; also acts on propionate and (very slowly) on butanoate.

thiol **1** *or (formerly)* **mercaptan** any organic compound containing –SH as the principal group directly attached to a carbon atom. **2** *or* **sulfhydryl** the (covalently linked) –SH group in any chemical compound.

+thiol *suffix (in organic chemical nomenclature)* indicating the presence of a **thiol** group attached to a carbon atom. *Compare* **mercapto+**.

thiolactomycin an antibiotic isolated from *Nocardia* spp. It selectively inhibits type II straight-chain fatty-acid synthases (i.e. the monofunctional enzyme system such as that in

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Escherichia coli) but not the type I enzymes (i.e. the multifunctional enzyme system such as that in *Saccharomyces cerevisiae*).

thiolase a commonly used but misleading generic name for certain enzymes of differing chain-length specificity within subsubgroup EC 2.3.1 (acyltransferases) that catalyse the **thiolysis** by coenzyme A of CoA thioesters of β-oxo fatty acids according to the general equation:

$$RCO{-}CH_2CO{-}CoA + CoA = RCO{-}CoA + CH_3CO{-}CoA.$$

Thiolases are thiol enzymes, their *S*-acyl derivatives being formed as intermediates in the reactions catalysed. Although the overall reactions are reversible, the equilibrium positions are greatly in favour of cleavage. These enzymes include: **acetyl-CoA *C*-acetyltransferase**; EC 2.3.1.9 and **acetyl-CoA C-acyltransferase**, EC 2.3.1.16.

thiolate **1** the anion, $R{-}S^-$, derived from a **thiol** (def. 1). **2** any salt of a thiol. **3** to introduce a thiol group into an organic compound. —**thiolation** *n.*

thiol proteinase *an old name for* **cysteine endopeptidase.**

thioltransacetylase A *see* **dihydrolipoamide *S*-acetyltransferase.**

thiolysis lysis of a covalent organic compound by a thiol; a reaction analogous to **alcoholysis** in which bond cleavage is mediated by nucleophilic attack by the –SH group of an alkanethiol. The term is applied in particular to the **thiolase**-catalysed cleavage of a β-oxoacyl-CoA by coenzyme A in each cycle of chain-length reduction during fatty-acid catabolism. —**thiolytic** *adj.*

thionein the apoprotein of a **metallothionein.**

thionin any of a group of small proteins, characterized by two conserved motifs, that occur in plants and are toxic to animals. Example, leaf thionin from barley (precursor): database code THN3_HORVU, 137 amino acids (14.65 kDa); the toxic principle is formed from amino-acid residues 29–34.

thionucleoside any *N*-glycoside of any **thiopurine** or **thiopyrimidine.**

thionucleotide any phosphoric ester of any **thionucleoside.**

thiopurine any **purine** in which a thiol group has replaced a hydroxyl group. *Compare* **mercaptopurine.**

thiopyrimidine any **pyrimidine** in which a thiol group has replaced a hydroxyl group.

thioredoxin any member of a widely occurring class of heat-stable hydrogen-carrier proteins of ≈12 kDa that serve as hydrogen donors in various reduction reactions, notably of ribonucleoside diphosphates to the deoxy analogues, and in the light-dependent reductive activation of various chloroplast enzymes (including a number of those in the pentose-phosphate cycle). Chloroplast thioredoxin occurs in two forms (designated *f* and *m*), which show specificity in their enzyme-activating properties; a third form (designated *c*), of unknown function, occurs outside chloroplasts. Thioredoxins can exist in disulfide (i.e. oxidized) and dithiol (i.e. reduced) states, interconversion being catalysed by ferredoxin–thioredoxin reductases. Example, thioredoxin 1 from *Anacystis nidulans*: database code THI1_ANANI, 106 amino acids (11.52 kDa). *See also* **thioredoxin reductase (NADPH).**

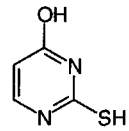
thioredoxin reductase (NADPH) EC 1.6.4.5; a flavoprotein (FAD) enzyme that catalyses the reaction:

$$NADPH + \text{oxidized thioredoxin} = NADP^+ + \text{reduced thioredoxin}.$$

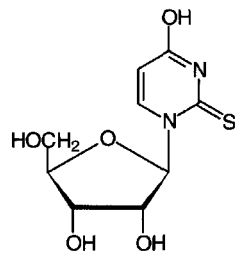
Example from *Escherichia coli*: database code TRXB_ECOLI, 320 amino acids (34.45 kDa); a homodimer.

thiotemplate mechanism *or* **protein thiotemplate mechanism** the mechanism of biosynthesis of *Bacillus brevis* peptide antibiotics, e.g. **gramicidin S** and **tyrocidin** A, in which the precursor amino acids, after activation, are bound as thioesters to the synthetase enzymes.

thiouracil *symbol*: Sur; 2-thiouracil; 4-hydroxy-2-mercaptopyrimidine; 4-oxy-2-thiopyrimidine; a naturally occurring thiopyrimidine, found in seeds of members of the cabbage family (e.g. *Brassica* spp.) and as a minor base in certain types of ribonucleic acid, especially transfer RNA (*see also* **thiouridine**). Thiouracil, 6-methylthiouracil, and 6-propylthiouracil are clinically useful for treatment of hyperthyroidism and thyrotoxicosis, their action being to inhibit biosynthesis of the thyroid hormones at the peroxidase-catalysed iodination and coupling steps.



thiouridine *symbol*: S *or* sU *or* Srd; either of two constitutional isomers occurring as minor nucleosides in certain types of ribonucleic acid, especially transfer RNA (tRNA): **2-thiouridine** (2-thiouracil riboside; 1-β-D-ribofuranosyl-4-oxy-2-thiopyrimidine; *symbol*: ^2S *or* s^2U), or its 5-methyl, 5-(methylaminomethyl), or 5-(methoxycarbonylmethyl) derivatives, which are found in some tRNA species in the first position of the anticodon; and **4-thiouridine** (4-thiouracil riboside; 1-β-D-ribofuranosyl-2-oxy-4-thiopyrimidine; *symbol*: ^4S *or* s^4U), which is found in some tRNA species elsewhere than in the anticodon.



2-thiouridine

third law of thermodynamics *see* **thermodynamics.**

thixotrope a gel that exhibits **thixotropy.**

thixotropy the property shown by certain fluids and gels of becoming less viscous when subjected to stress, e.g. by shaking or stirring, and of becoming more viscous again when the stress is relieved. —**thixotropic** *adj.*

Thr *symbol for* a residue of the α-amino acid L-threonine (alternative to T).

THR a gene family encoding thyroid receptors; part of a superfamily including receptors for steroids, retinoic acid, and vitamin D_3; *see* ***erbA.***

threitol active erythritol, *threo*-1,2,3,4-tetrahydroxybutane, *threo*-1,2,3,4-butanetetrol; an enantiomeric pair of polyols, configurationally isomeric with **erythritol.** D-Threitol occurs in certain fungi, e.g. the honey fungus, *Armillaria mellea.*

threo- a configurational prefix to the systematic name of a polyhydric alcohol, especially of a monosaccharide, used to indicate the particular stereochemical configuration of a set of two contiguous >CHOH groups that occurs in D-threose (see ***threose*** for structure) or L-threose, e.g. D-*threo*-2-pentulose for D-xylulose. *Compare* ***erythro-.***

threoninate **1** threonine anion; the anion, $CH_3{-}CH(OH){-}CH(NH_2){-}COO^-$, derived from **threonine.** **2** any salt containing threonine anion. **3** any ester of threonine.

threonine *the trivial name for* α-amino-β-hydroxybutyric acid; (2*R**,3*S**)-2-amino-3-hydroxybutanoic acid; $CH_3{-}CH(OH){-}CH(NH_2){-}COOH$; an α-amino acid with two chiral centres.

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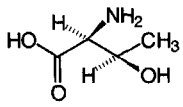
Because molecules of threonine possess a second chiral centre, at C-3, in addition to the chiral centre at C-2 common to all α-amino acids other than glycine, the enantiomers L-threonine, (2*S*,3*R*)-2-amino-3-hydroxybutanoic acid (*symbol*: T *or* Thr), and D-threonine, (2*R*,3*S*)-2-amino-3-hydroxybutanoic acid (*symbol*: D-Thr *or* DThr), are diastereoisomeric with those of **allothreonine**, (2*R**,3*R**)-2-amino-3-hydroxybutanoic acid. [*Note*: The enantiomers of threonine may also be named semi-systematically as derivatives of threose: L_g-threonine in amino-acid nomenclature is synonymous with 2-amino-2,4-dideoxy-D_g-threonic acid in carbohydrate nomenclature, and D_s-threonine with 2-amino-2,4-dideoxy-L_g-threonic acid (the subscript letters d or g being added to the configurational prefixes where there might be uncertainty regarding the reference centre of chirality; *see* **D/L convention**).] L-Threonine is a coded amino acid found in peptide linkage in proteins; codon: ACA, ACC, ACG, or ACU. In mammals it is an essential dietary amino acid, is glucogenic, and its deficiency causes fatty liver. The fungal toxins phalloidin and phalloin contain one residue of D-threonine per molecule.



L-threonine

threonine aldolase *see* **glycine hydroxymethyltransferase**.

threonine dehydratase EC 4.2.1.16; *systematic name*: L-threonine hydro-lyase (deaminating); *other names*: threonine deaminase; L-serine dehydratase; serine deaminase. A pyridoxal-phosphate enzyme that catalyses a reaction between L-threonine and water to form 2-oxobutanoate, NH_3, and water; it acts also on L-serine. There are two types (examples from *Escherichia coli*): type 1 is responsible for the first step of isoleucine biosynthesis (serine is an alternative but poorer substrate): database code THD1_ECOLI, 514 amino acids (56.13 kDa); type 2 is a catabolic enzyme that acts on both serine and threonine, and is properly considered as a hydroxy-amino-acid deaminase: database code THD2_ECOLI, 329 amino acids (35.19 kDa).

threonine synthase EC 4.2.99.2; *systematic name*: *O*-phospho-L-homoserine phospho-lyase (adding water). A pyridoxal-phosphate enzyme that catalyses the formation of L-threonine from *O*-phospho-L-homoserine and water with release of orthophosphate. Example from *Escherichia coli*: database code THRC_ECOLI, 428 amino acids (47.06 kDa); it shows sequence homology with the serine dehydratase/threonine dehydratase group.

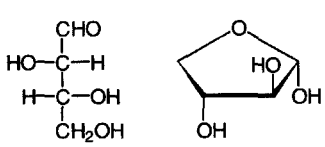
threoninium threonine cation; the cation, CH_3–$CH(OH)$–$CH(NH_3^+)$–$COOH$, derived from **threonine**.

threonino the alkylamino group, CH_3–$CH(OH)$–$CH(COOH)$–NH–, derived from **threonine**.

threonin-*O*^{3}-yl the alkyloxy group, $HOOC$–$CH(NH_2)$–$CH(CH_3)$–O–, derived from **threonine**.

threonyl the acyl group, CH_3–$CH(OH)$–$CH(NH_2)$–CO–, derived from **threonine**.

threose *the trivial name for* the aldotetrose *threo*-tetrose; it has D and L enantiomers, which are respectively diastereoisomeric with those of erythrose. *See also* **threo-**.



α-D-threose

threshold the value that must be achieved or exceeded for an effect to become discernible. For example, the **kidney threshold of excretion**, for any substance, is the plasma concentration at which not all of the substance that appears in the filtrate can be reabsorbed, so that it appears in the urine.

THRF *abbr. for* thyrotropic hormone releasing factor; i.e. **thyrotropin-releasing hormone**.

THRH *abbr. for* thyrotropic hormone releasing hormone; i.e. **thyrotropin-releasing hormone**.

thrombin EC 3.4.21.5; *other name*: fibrinogenase; a serine proteinase, M_r 33 700-33 900, the natural coagulant of **fibrinogen**. Thrombin appears in the blood following activation of the coagulation system, as a result of proteolysis of **prothrombin**. It catalyses the preferential cleavage of Arg-|-Gly, activating fibrinogen to **fibrin** and releasing fibrinopeptides A and B. Its effects are mediated by the **thrombin receptor**. *See also* **blood coagulation**.

thrombin receptor a protein of platelets and vascular endothelial cells that binds **thrombin** and mediates its intracellular effects. It is a G-protein-coupled receptor. Example from human (precursor): database code THRR_HUMAN, 425 amino acids (47.35 kDa); this is a glycoprotein; the signal peptide comprises amino acids 1–26, and amino acids 27–41 are removed by thrombin, after which the new N terminus functions as a tethered ligand and the receptor is thereby activated.

thrombocyte *an alternative name for* **platelet**.

thrombogenic **1** tending to promote the formation of a blood clot (i.e. a **thrombus**). **2** having a precursor function for, or tending to promote, the formation of **thrombin**.

β-thromboglobulin a homotetramer of a peptide derived from **platelet basic protein precursor** by removal of the first four N-terminal residues from **LA-PF4**. It is released by activated platelets. It belongs to the intercrine α family (*see* **chemokine**) and mediates a number of actions in the inflammatory response, including chemotaxis of leukocytes.

thrombokinase *an alternative name for* factor Xa; *see* **blood coagulation**.

thrombolysis the degradation of a blood clot (i.e. **thrombus**) as a result of physiological or pharmacological action.

thrombolytic **1** tending to promote **thrombolysis**. **2** a drug or other substance promoting thrombolysis.

thrombomodulin *abbr.*: TM; *other name*: fetomodulin; a specific endothelial cell receptor that forms a 1:1 stoichiometric complex with thrombin, the complex being responsible for conversion of protein C to activated protein C. It is a type I membrane protein. Example (precursor) from human: database code TRBM_HUMAN, 575 amino acids (60.26 kDa).

thromboplastin *an alternative name for* factor III; *see* **blood coagulation**.

thrombospondin *or* **glycoprotein G** a thrombin-sensitive major glycoprotein located in the alpha granules of human platelets. It is secreted on thrombin activation and binds to the platelet membrane in the presence of Ca^{2+}. It is an adhesion molecule that mediates cell–cell and cell–matrix interactions and can bind to fibrinogen, fibronectin, laminin, and type V collagen. It is a trimeric disulfide-linked protein and contains three types of repeating amino-acid sequence; the first is 57 amino acids long and shows homology with circumsporozoite protein from a malarial parasite; the second is 50–60 amino acids long and shows homology with **epidermal growth factor**; the third occurs as a continuous eightfold repeat of a 38-residue sequence; structural homology with **calmodulin** indicates that these repeats constitute multiple calcium-binding sites. Example, human thrombospondin 1 precursor: database code TSP1_HUMAN, 1170 amino acids (129.27 kDa). There are at least three such related proteins in humans.

thromboxane any of a class of **prostanoids** synthesized by **thromboxane-A synthase** (EC 5.3.99.5) from prostaglandin H (the product of prostaglandin-endoperoxide synthase) as thromboxane A (TXA). Depending on whether the substrate of the enzyme is dihomo-(6,9,12)-linolenate, arachidonate, or eicosa-

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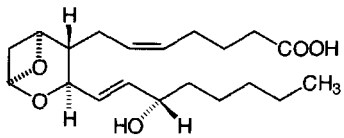
5,8,11,14,17-pentaenoate, the product is TXA_1, TXA_2, or TXA_3 respectively. TXA_2 is the major thromboxane *in vivo*. It is synthesized in platelets when these are activated by other aggregatory compounds and strongly reinforces the aggregatory reaction. Its biological lifetime is a few minutes, TXA_2 being converted to the inactive metabolite thromboxane B_2 (TXB_2) by addition of water across the endoperoxide. Oxidation of the 11-hydroxy group of TXB_2 to an oxo group yields 11-dehydro-thromboxane A_2, a major long-lived metabolite in human plasma, useful for measurement as an index of thromboxane production. Beta-oxidation of TXB_2 yields 2,3-dinor-thromboxane B_2, the major human urinary metabolite. **Dideoxy-epoxymethanoprostaglandin $F_{2\alpha}$** is a stable analogue that mimics TXA_2.



TXA_2

thromboxane-A synthase EC 5.3.99.5; *other names*: thromboxane synthase; thromboxane synthetase (*abbr.*: TXS); an enzyme that catalyses the formation from (5*Z*,13*E*)-(15*S*)-9α,11α-epidioxy-15-hydroxyprosta-5,13-dienoate of (5*Z*,13*E*)-(15*S*)-9α,11α-epoxy-15-hydroxythromba-5,13-dienoate (**thromboxane** A_2). It is a heme-thiolate protein. 1-(7-Carboxyheptyl)imidazole and benzylimidazole inhibit thromboxane-A synthase, as does the drug U-63557A, sodium furegrelate. Example from human: database code THAS_HUMAN, 533 amino acids (60.42 kDa).

thrombus (*pl.* **thrombi**) a blood clot forming within a blood vessel. Thrombus formation may occur as a normal response during physiological blood coagulation. It may also occur pathologically, triggered by **atheroma**, and is the immediate cause of ischemia in a heart attack. Thrombi may also form, especially in veins, at other times, e.g. after surgery, and if they reach the lungs cause pulmonary embolism.

Thunberg method an early method for detecting and estimating **dehydrogenases** depending on the rate and extent of decolorization of Methylene Blue in solution in the presence of dehydrogenase and substrate. The apparatus, known as a **Thunberg tube**, consists of a stoppered glass tube (sometimes with a side-arm for addition of reagents) that may be evacuated through the stopper, and then sealed by a twist of the stopper. [After Torsten Ludvig Thunberg (1873–1952), Swedish physiological chemist.]

Thx *symbol for* a residue of the α-amino acid and thyroid hormone L-thyroxine (alternative to T_4).

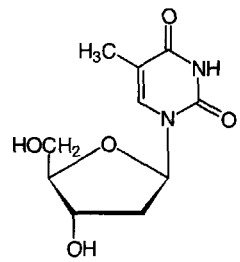
Thy *symbol for* a residue of the pyrimidine base thymine (alternative to T).

Thy-1 an allelic variable molecule, encoded on mouse chromosome 9, that is present on all T lymphocytes and also occurs in brain. It is a GPI-anchored membrane glycoprotein of the immunoglobulin superfamily, with a simple structure homologous to the **variable region** of an immunoglobulin molecule. Example (precursor) from human: database code THY1_HUMAN, 161 amino acids (17.94 kDa). *See also* **thymopoietin**.

thylakoid a saclike vesicle that bears the photosynthetic pigments in photosynthetic organisms. In prokaryotes the thylakoids are of various shapes and are attached to the plasma membrane. In eukaryotes they are flattened, membrane-bound disclike structures located in the **chloroplasts**; in the chloroplasts of higher plants the thylakoids form dense stacks called **grana**. Isolated thylakoid preparations can carry out photosynthetic electron transport and the associated phosphorylation.

thymic hormones *see* **thymopoietin, thymosin**.

thymidine *or* **deoxyribosylthymine** *symbol*: dT *or* dThd; thymine 2′-deoxyriboside; 1-(2-deoxy-β-D-ribofuranosyl)-5-methyluracil; a deoxynucleoside very widely distributed but occurring almost entirely as phosphoric esters in deoxynucleotides and deoxyribonucleic acid, DNA. *Compare* **ribothymidine**. Because thymidine is absent from ribonucleic acid, the incorporation of radioisotope-labelled thymidine into cells has been made the basis of a procedure frequently used for measuring the rates of DNA synthesis and cell growth.



thymidine 5′-diphosphate *symbol*: dThd5′*PP* *or* ppdT; *the recommended name for* thymidine diphosphate (*abbr.*: dTDP), 5′-diphosphothymidine, 5′-thymidylyl phosphate, thymidine 5′-(trihydrogen diphosphate). It is an intermediate in the formation of thymidine 5′-triphosphate from thymidine 5′-phosphate. Derived compounds are the rare **nucleosidediphosphosugars** thymidinediphosphorhamnose and its biosynthetic precursor thymidinediphosphoglucose.

thymidine kinase EC 2.7.1.21; *systematic name*: ATP:thymidine 5′-phosphotransferase; an enzyme that catalyses the phosphorylation by ATP of thymidine to thymidine 5′-phosphate with release of ADP. It acts on thymidine taken into a cell, or on free thymidine released within a cell, as a first step in its further metabolism. Mitochondrial and cytosolic forms are known, the latter showing much greater activity in proliferating than in resting cells. Example from herpes simplex type 2: database code KITH_HSV23, 375 amino acids (40.32 kDa).

thymidine monophosphate *abbr.*: dTMP; *an alternative name for* any **thymidine phosphate**, but in particular for thymidine 5′-phosphate, especially when its distinction from thymidine (5′-)diphosphate and thymidine (5′-)triphosphate requires emphasis.

thymidine phosphate *symbol*: dThd*P*; thymidine monophosphate (*abbr.*: dTMP); any phosphoric monoester or diester of thymidine. There are two monoesters – thymidine 3′-phosphate and **thymidine 5′-phosphate** – and one diester – thymidine 3′,5′-phosphate – although thymidine 5′-phosphate is the ester commonly denoted (the locant being omitted if no ambiguity may arise). Thymidine 3′-phosphate (*symbol*: dThd3′*P*), also named thymidine 3′-monophosphate (*abbr.*: 3′dTMP) *or* 3′-thymidylic acid, is released from deoxyribonucleic acid by the action of certain endo- or exonucleases, e.g. deoxyribonuclease II (EC 3.1.22.1) or spleen exonuclease (EC 3.1.16.1). The monophosphoric diester thymidine 3′,5′-phosphate (*symbol*: dThd-3′,5′-*P*), also named thymidine 3′,5′-(cyclic)phosphate *or* cyclic thymidine 3′,5′-monophosphate (*abbr.*: 3′,5′-cyclic dTMP *or* cyclic dTMP *or* cdTMP), has been isolated as an intermediate formed during the acid hydrolysis of deoxyribonucleic acid but is not known to be of significance otherwise.

thymidine 3′-phosphate *see* **thymidine phosphate**.

thymidine 3′,5′-phosphate *see* **thymidine phosphate**.

thymidine 5′-phosphate *or* **5′-thymidylic acid** *or* **5′-phosphothymidine** *or* **5′-*O*-phosphonothymidine** *symbol*: dThd5′P; *alternative recommended names for* thymidine monophosphate (*abbr.*: dTMP), thymidine 5′-(dihydrogen phosphate), thymine (mono)deoxynucleotide. (The locant is commonly omitted if there is no ambiguity as to the position of phosphorylation.) It

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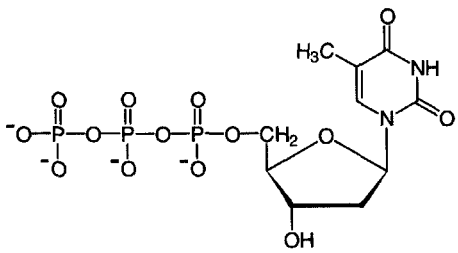
is synthesized (very indirectly) from **uridine 5′-phosphate**, its immediate precursor being 2′-deoxyuridine 5′-phosphate – *see* **thymidylate synthase**. In addition, resynthesis of dTMP from free thymidine formed by degradation of DNA can be effected via a **salvage pathway**.

thymidine phosphorylase *see* **pyrimidine-nucleoside phosphorylase**.

thymidine 5′-triphosphate *symbol*: dThd5′*PPP or* pppdT; *the recommended name for* thymidine triphosphate (*abbr.*: dTTP), 5′-triphosphothymidine, 5′-thymidylyl diphosphate, thymidine 5′-(tetrahydrogen triphosphate); a substrate for DNA synthesis. It is formed from thymidine 5′-phosphate by the successive action of nucleoside-phosphate kinase (EC 2.7.4.4) and nucleoside-diphosphate kinase (EC 2.7.4.6), which transfer in turn the terminal phosphoric residues from two molecules of adenosine 5′-triphosphate.



thymidyl either of the chemical groups formed by the loss of a 3′- or a 5′-hydroxyl group from the deoxyribose moiety of thymidine.

thymidylate **1** either the monoanion or the dianion of thymidylic acid. **2** any mixture of thymidylic acid and its anions. **3** any salt or ester of thymidylic acid.

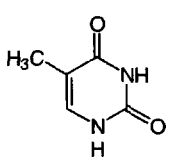
thymidylate synthase EC 2.1.1.45; *systematic name*: 5,10-methylenetetrahydrofolate:dUMP *C*-methyltransferase; an enzyme responsible for the formation of thymidylate, dTMP, by the *de novo* pathway. It catalyses reductive methylation of 2′-deoxy-5′-uridylate, dUMP, by reaction with 5,10-methylenetetrahydrofolate to form dihydrofolate and dTMP. (The dihydrofolate thus formed is reduced again to tetrahydrofolate by **dihydrofolate reductase**.) Thymidylate synthase is important as a target for the antineoplastic agents **fluorouracil** and fluorodeoxyuridine. These drugs are metabolized to fluorodeoxyuridylate, which is a potent irreversible inhibitor of the enzyme. Example from *Escherichia coli* (homodimer): database code TYSY_ECOLI, 264 amino acids (30.44 kDa); 3-D structure known; five motifs. *See also* **thymineless death**.

thymidylic acid *the trivial name for* any phosphoric monoester of thymidine. The position of the phosphoric residue on the deoxyribose moity of a given ester may be specified by a prefixed locant – *see* **thymidine phosphate**. However, 5′-thymidylic acid is the ester commonly denoted, its locant usually being omitted if no ambiguity may arise. 5′-Thymidylic acid is also an alternative recommended name for **thymidine 5′-phosphate**.

thymidylyl the thymidine[mono]phospho group; the acyl group derived from **thymidylic acid**.

thymin *a former name for* **thymopoietin**.

thymine *symbol*: T *or* Thy; 5-methyluracil; 2,4-dihydroxy-5-methylpyrimidine; one of the two major pyrimidine bases present (as thymidine) in DNA but not found in RNA other than (as ribothymidine) in transfer RNA, where it is a minor base.



thymine dimer a **pyrimidine dimer** formed within a DNA strand from two adjacent thymine residues by **photodimerization**. It is most commonly of the cyclobutadipyrimidine type.

thymineless death the death of an animal or bacterial cell following a period of thymine (or thymidylate) deprivation. Although such a deprived cell may continue to produce protein and RNA, it can no longer synthesize DNA in the absence of thymidylate, and it eventually loses its vitality and dies, perhaps because it is also unable to repair altered or damaged DNA. The phenomenon may be demonstrated with a thymine-requiring auxotrophic bacterial mutant by omitting thymine from the suspending medium, or with any cell by adding **fluorouracil** or its metabolite fluorodeoxyuridine, with consequent inhibition of **thymidylate synthase**. A rapidly metabolizing animal cell, such as a tumour cell, is particularly susceptible to thymineless death.

thymine deoxyriboside *an alternative name for* **thymidine**.

thymine riboside *an alternative name for* **ribothymidine**.

thyminose *a former name for* 2-deoxy-D-ribose (*see* **deoxyribose**).

thymo+ *comb. form* of, or pertaining to, the thymus.

thymocyte *(sometimes)* any **lymphocyte** found in the thymus.

thymocyte mitogenic factor *abbr.*: TMF; *an alternative name for* **interleukin 2**.

thymocyte-stimulating factor *abbr.*: TSF; *an alternative name for* **interleukin 2**.

thymoma a tumour of thymic tissue.

thymonuclease *another name for* **deoxyribonuclease I**.

thymonucleic acid *an alternative term for* **thymus nucleic acid**.

thymopentin a synthetic pentapeptide that corresponds to residues 32–36 of **thymopoietin**.

thymopoietin *abbr.*: TP; any one of three polypeptide hormones that result from alternative splicing of the same gene, and originally isolated from bovine thymus. They have pleiotropic actions on prothymocytes, inducing expression of the differentiation antigens such as **Thy-1**, and are important in T-cell development and function. They were discovered in studies on myasthenia gravis and impair neuromuscular transmission after injection in mice, due to an effect on the nicotinic acetylcholine receptor. A synthetic pentapeptide corresponding to positions 32–36, named **thymopentin** and with the sequence Arg-Lys-Asp^{34}-Val-Tyr, has full activity. **Splenin**, a corresponding peptide in spleen, contains a similar pentapeptide, called **splenopentin**; bovine splenin has Glu in place of Asp^{34}, and human splenin has Ala in the corresponding position. These replacements affect the biological activity. Thymopoietin was formerly known as thymin.

thymosin any of several related polypeptide hormones of thymic origin that are involved in differentiation of T lymphocytes in the thymus. They include α_1 and β_4 thymosins, which are of known structure. Thymosin β_4 (human, bovine, rat) has the sequence SDKPDMAEIEKFDKSKLKKTETQEKNPLPSKETIEQEKQAGES.

thymulin a zinc-requiring immunomodulatory thymic nonapeptide hormone known to induce intra- and extra-thymic T-cell differentiation. Its level is decreased in immunodeficiency and in autoimmune disease.

thymus (gland) a bilobed glandular organ located in the posteroventral part of the neck. In mammals the thymus is encapsulated and divided into lobules, each lobule consisting of cortex and medulla; the cortex consists mainly of lymphocytes (thymocytes). The thymus is responsible for populating the blood, lymph, and thymus-dependent areas with **T lymphocytes** during the neonatal period. The thymus is large at birth but diminishes in size with increasing age and may be difficult to identify in adults. It is important in **cell-mediated immunity**. — **thymic** *adj.*

thymus nucleic acid *a former name for* **deoxyribonucleic acid**. It was so termed because the thymus gland was found to be a particularly rich source of nucleic acid of a type that was thought at the time to be characteristic of animal tissues and

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that was distinct from the type believed to be characteristic of plant tissues and known as **yeast nucleic acid**.

thyro+ *comb. form* of, or pertaining to, the **thyroid gland**.

thyrocalcitonin *see* **calcitonin**.

thyroglobulin a protein in the **thyroid gland**, tyrosyl residues of which are modified to form the principal thyroid hormone, **thyroxine**, which is released by proteolysis. Thyroglobulin, a dimer of molecular mass about 660 kDa, is the main constituent of the so-called colloid of the thyroid follicles. Iodination of certain tyrosyl residues results in the formation of 3,5-iodotyrosyl residues; there is then transfer of the iodinated phenolic moiety of one of these tyrosyls (in the free form this would be a 2,6-iodophenyl group) to the phenolic oxygen of another iodinated tyrosyl to form a tetraiodo compound which, on release by proteolysis, is thyroxine (T_4) (some triiodo forms are also produced). The proteolysis occurs as colloid migrates from the basal to the apical surfaces of the thyroid cell. Example (precursor) from human: database code THYG_HUMAN, 2767 amino acids (304.45 kDa). The colloid containing the modified thyroglobulin is taken into vesicles by phagocytosis to form periodic acid–Schiff positive (PAS) vesicles. Dense granules containing proteolytic enzymes then fuse with the vesicles to digest the thyroglobulin with the loss of PAS-positive material. The vesicles containing triodothyronine and thyroxine are then extruded.

thyroidectomy the surgical removal of the thyroid gland.

thyroid gland a ductless gland, located near the larynx in most species, that secretes the hormones **thyroxine** and **triiodothyronine**. Thyroid tissue is confined to vertebrates. The gland contains closely packed follicles, or acini, each consisting of a sac that has a peripheral single layer of cuboidal follicular cells forming an epithelium on an outer basement membrane; the centre of the follicle is occupied by a colloid of which the major component is **thyroglobulin**. This is synthesized and secreted into the colloid space by the follicular cells; microvilli extend from the apical surface of the follicular cells into the colloid. The thyroid also contains parafollicular cells, or C cells, that synthesize **calcitonin**. Enlargement of the thyroid in iodine deficiency is the basis of **goitre**. The thyroid concentrates iodide, a property that can be used for thyroid imaging, and for the treatment of cancer of the thyroid.

thyroid hormone either of the compounds secreted by the **thyroid gland**, namely **thyroxine** and **triiodothyronine**.

thyroid hormone receptor a nuclear receptor for **triiodothyronine** that mediates the effects of thyroid hormones on cells. These receptors bind triiodothyronine and directly regulate gene expression. The proteins belong to a superfamily of eukaryotic transcription factors and the steroid/thyroid/retinoic acid family of nuclear receptors for hormones. The ligand-binding domain is in the C-terminal region, the zinc-finger DNA-binding domain in a central region, and a function-modulating domain in the N-terminal region. Binding of hormone induces changes in receptor conformation that control transcriptional activation and repression, and also regulates homo- or heterodimerization. In the absence of ligand, these receptors repress basal gene expression, probably through co-repressor proteins. Example, α-1 receptor from *Mus musculus*: database code THA1_MOUSE, 410 amino acids (46.79 kDa).

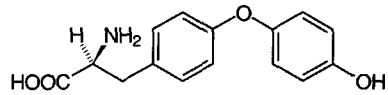
thyroid hormone either of the compounds secreted by the **thyroid gland**, namely **thyroxine** and **triiodothyronine**.

thyroid response element *abbr.*: TRE; *see* **response element**.

thyroid-stimulating hormone *abbr.*: TSH; *recommended name*: thyrotropin; *other name*: thyrotropic hormone; a hormone, secreted by the adenohypophysis, that stimulates the activity of the thyroid gland. The bovine hormone is a glycoprotein, M_r 28 300, and a heterodimer of two chains, α (M_r 13 600) and β (M_r 14 700). The α chain has an amino-acid sequence identical with that of the α chain of **luteinizing hormone** of the same species. TSH increases the uptake of iodide by the thyroid, increases the rate of conversion of diiodotyrosine to thyroxine, and increases the release of thyroid hormones from the thyroid. The release of TSH from the adenohypophysis is influenced by **thyrotropin-releasing hormone**. Examples, α chain (precursor) from human: database code GLHA_HUMAN, 116 amino acids (13.06 kDa); β chain (precursor) from human: database code TSHB_HUMAN, 138 amino acids (15.59 kDa).

thyroliberin *recommended name for* **thyrotropin-releasing hormone**.

thyronine 4-(4-hydroxyphenoxy)phenylalanine; the structure from which thyroid hormones may be notionally derived by iodination. It is not naturally occurring, even in bound form, since in the synthesis of thyroid hormones the tyrosyl residues of thyroglobulin are iodinated before addition of the further phenolic group (*see* **thyroglobulin**).



thyrotoxicosis *see* **hyperthyroidism**.

thyrotroph a thyrotropic cell.

thyrotrophic having the effect of nourishing the thyroid gland, stimulating its growth and maintaining its size.

thyrotropic *or (esp. Brit.)* **thyrotrophic** having a modulating effect on the thyroid gland, especially in stimulating the synthesis of thyroid hormones. *See* **thyrotropin**.

thyrotropic hormone *an alternative name for* **thyroid-stimulating hormone**.

thyrotropic hormone releasing factor (*abbr.*: THRF) *or* **thyrotropic hormone releasing hormone** (*abbr.*: THRH) *an alternative name for* **thyrotropin-releasing hormone**.

thyrotropin *the recommended name for* **thyroid-stimulating hormone**.

thyrotropin receptor an integral membrane protein that binds thyrotropin (i.e. **thyroid-stimulating hormone**) and mediates its intracellular effects. It is a G-protein-linked receptor, with different forms produced by alternative splicing. Example from human (precursor): database code TSHR_HUMAN, 764 amino acids (86.70 kDa). Mutations are associated with hyperfunctioning thyroid adenomas. The hyperthyroidism of **Graves' disease** is thought to be due to the presence in the blood of these patients of autoantibodies that stimulate the thyroid through the thyrotropin receptor.

thyrotropin-releasing factor *abbr.*: TRF; *an alternative name for* **thyrotropin-releasing hormone**.

thyrotropin-releasing hormone *abbr.*: TRH; *recommended name*: thyroliberin; *other names*: thyrotropin-releasing factor (*abbr.*: TRF); thyrotropic hormone releasing factor (*abbr.*: THRF); thyrotropic hormone releasing hormone (*abbr.*: THRH); a hormone, released by the mammalian hypothalamus into the hypophyseal–portal circulation in response to neural and/or chemical stimuli, that regulates the secretion of **thyroid-stimulating hormone** (TSH) by the adenohypophysis. It has a wide distribution, being present not only in primitive vertebrates but also in *Amphioxus* (a provertebrate) and in nerve ganglia of snail. It is the tripeptide pyroGlu-His-Pro-NH_2, the cyclized glutamate and intact prolylamide being essential for activity. It is synthesized as part of a large prohormone that has six repeats of the TRH sequence. TRH is present in many other parts of the brain, in pancreatic islets, and in the gastrointestinal tract; it probably serves widely as a neurotransmitter or neuromodulator, being known in mammals to alter sleep patterns, increase motor activity, increase blood pressure, and affect norepinephrine turnover, among many activities. Its regulation of TSH secretion is controlled by the pituitary–thyroid axis.

thyroxine *abbr.*: Thx *or* T_4; 4-(4-hydroxy-3,5-diodophenoxy)-3,5-diodophenylalanine; 3,3′,5,5′-tetraiodothyronine; the main hormone secreted by the thyroid gland, although its ac-

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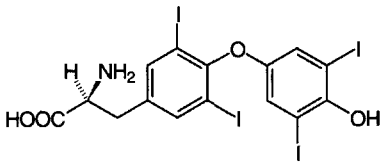
tivity is lower than that of **triiodothyronine** (T_3). Its synthesis from L-tyrosyl residues of **thyroglobulin** means that the L-isomer is the naturally occurring form. Thyroxine is essential for normal metabolism and physical development. It stimulates the metabolic rate, causing increased oxygen consumption and heat production in tissues. Although in humans the plasma levels of T_4 are 20- to 50-fold higher than those of T_3, T_4 is converted to T_3 in tissues and the effects are thought to be mediated by T_3 binding to receptors in the cell nucleus (chromatin fraction), leading to mRNA and protein synthesis. The normal range in human blood is 60–150 nmol L^{-1} (total of bound and free), 9–26 pmol L^{-1} (free). The chemical constitution of thyroxine was deduced by the British biochemist Sir Charles R. Harington (1897–1972), and confirmed by synthesis (1927).



thyroxine-binding globulin *abbr.*: TBG; a major thyroid hormone transport protein found in mammalian serum. It is synthesized in liver, and variations in its concentration in serum result in similar variations in the level of circulating thyroid hormones. Alterations in its affinity for thyroid hormone also affect circulating thyroid hormone levels, decreased affinity being accompanied by decreased serum concentration. In the human, this variation may result from non-thyroidal illness, the presence of drugs (salicylates and phenytoin block thyroid-binding sites), or genetic variation, many variants being known, and listed in the example from human: database code THBG_HUMAN, 415 amino acids (46.32 kDa).

Ti *symbol for* titanium.

tight coupling a term applied to mitochondrial function implying a high degree of efficiency in the yield of ATP (or other functional response) in relation to electron flow. The nearer the yield approaches the optimal value, the tighter the coupling is said to be. Tight coupling is obtained in isolated mitochondria only if gentle procedures, preserving membrane integrity, are employed during isolation. *See also* **chemiosmotic coupling hypothesis**, **phosphorus:oxygen ratio**.

tight junction *or* **zona occludens** *(in vertebrate tissues)* a belt-like region of very close contact between the plasma membranes of adjacent cells, such that the intercellular space is completely occluded. Tight junctions occur in epithelia and brain endothelia, and are effective barriers to the passage of water and solutes. *Compare* **gap junction**.

tight turn *see* **beta turn**.

time *symbol*: *t*; one of the seven SI base physical quantities, usually indicating duration or a precise moment. The SI base unit of time is the **second**.

time constant a characteristic time taken by a system or a process to respond to a perturbation.

time course a graph plot of a parameter (that changes with time) scaled on the ordinate and time scaled on the abscissa.

time-resolved fluorescence spectrometry a method in which a sample is irradiated using a laser delivering a short (sub-nanosecond) pulse of light, after which the exponential decay of fluorescence is measured using a photomultiplier. The sensitivity of detection must be at the single photon level ('single photon counting'), and fluorescence lifetimes as short as a few nanoseconds can be determined. However, a disadvantage of the technique is that many measurements over possibly several hours may be needed to obtain reliable and sufficient data. *See also* **steady-state fluorescence anisotropy**.

TIMP *abbr. for* tissue inhibitor of metalloproteases; any of a group of proteins that inhibit metalloproteinases. An example is TIMP-1, also known as EPA (erythroid potentiating activity), a protein that mediates erythropoiesis. It forms complexes with enzymes such as collagenases, bringing about irreversible inactivation. Example (precursor) from human: database code TIM1_HUMAN, 207 amino acids (23.14 kDa). *See also* **matrix metalloproteinase**.

tintometer an apparatus formerly used for determining the colour of a solution by comparison with a graded colour scale.

Ti plasmid *abbr. for* tumour-inducing plasmid; any of a class of large conjugative plasmids found in the soil bacterium *Agrobacterium tumefaciens* and responsible for **crown-gall disease** of broad-leaved plants – a segment of the Ti plasmid, the **T-DNA**, is found in the genome of the tumour tissue of affected plants. With appropriate modifications the Ti plasmid can carry foreign DNA sequences of any desired kind into the genome of a susceptible plant.

Tiselius, Arne Wilhelm Kaurin (1902–71), Swedish protein chemist; Nobel Laureate in Chemistry (1948) 'for his research on electrophoresis and adsorption analysis, especially for his discoveries concerning the complex nature of the serum proteins'.

Tiselius apparatus an apparatus for performing **moving boundary electrophoresis** in which there is a U-tube with sliding joints. This enables the protein (or other) solution and the buffer to be placed in separate parts of the U-tube and sharp boundaries made between them when the parts are slid into position to complete the U-tube.

tissue any collection of cells that is organized to perform one or more specific function. *Compare* **organ**.

tissue culture **1** the technique or process of growing or maintaining tissue cells (**cell culture**), whole organs (**organ culture**), or parts of an organ, from an animal or plant, in artificial conditions. **2** any living material grown or maintained by such a technique.

tissue extract *an alternative name for* factor III; *see* **blood coagulation**.

tissue factor *abbr.*: TF; a transmembrane glycoprotein (eight motifs), also known as factor III, that initiates **blood coagulation** by forming a complex with factor VII or VIIA. The complex activates factors IX or X. Tissue factor plays a role in normal hemostasis by initiating cell-surface assembly and propagation of the coagulation protease cascade. Example from human (precursor): database code TF_HUMAN, 295 amino acids (33.03 kDa).

tissue grinder any device for disrupting tissue by a crushing or shearing action. The term may embrace devices ranging from a meat grinder (mincer), mechanical pestle and mortar, or mill, to the more precise **Potter–Elvehjem homogenizer** or the **Dounce homogenizer**.

tissue kallikrein *see* **kallikrein**.

titer *the US spelling of* **titre**.

titin *or* **connectin** a giant protein that forms a single molecule elastic filament extending from the M line to the Z line in the striated muscle sarcomere and is one of the largest polypeptides yet described. The sequence consists mainly of repeats of two types of approximately 100-amino-acid motifs, known as class I and class II that show homology to the fibronectin type-III domain and **immunoglobulin superfamily** C2 domain, respectively. There is also a domain characteristic of protein kinases near the C terminus. It is thought to play an important role in sarcomere alignment during muscle contraction. Example from human: database code HSTITIN, 4650 amino acids (521.48 kDa). *See also* **twitchin**.

titratable acidity **1** a measure of the acidity of a urine sample, expressed as the volume of 0.1-M NaOH required to neutralize, usually to a phenolphthalein endpoint, a 24-hour volume of urine. **2** a measure of the acidity of any solution, etc.

titrate **1** to add acid of known concentration to base of unknown concentration (or vice versa) until the point of equivalence is reached, from which can be determined the con-

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centration of the unknown. **2** more generally, to add any standard solution to an unknown until some detectable equivalence point is reached, enabling the amount of the unknown to be determined. **3** (*esp. in microbiology or immunology*) to determine the maximum dilution at which activity can be detected. *See* **titre** (def. 2). —**titratable** *adj.*; **titration** *n.*

titration curve originally, a curve relating pH to the equivalents of strong base added per equivalent of acid in the solution. Similar curves are obtained when the logarithm of ligand concentration is plotted against the degree of association (or dissociation) of a ligand to its acceptor, or when redox potential is plotted against the degree of oxidation (or reduction) of a redox system.

titration p*K* *symbol*: p*G*; a kind of **p*K*** that characterizes the titration curve of a multibasic acid. If this acid has *n* hydrons that titrate over the pH range of interest, then its titration curve is identical to that of an equimolar mixture of *n* (hypothetical) monobasic acids. The p*K* values of these acids are the titration p*K* values of the multibasic acid. They differ little from the **molecular p*K*** values if the differences between sequential molecular values exceed unity. *See also* **group p*K***.

titre *or (esp. US)* **titer** **1** a value found by titration; *see* **titrate** (def. 1, 2). **2** *(in microbiology and immunology)* a measure of the concentration or activity of an active substance, e.g. an antibody, in a solution, usually expressed as the highest dilution of the solution in which the activity can be detected. By convention, if the highest dilution giving activity is 100-fold, the titre is said to be 100.

titrimetry the technique of measurement by titration, particularly using instrumentation and automation.

Tl *symbol for* thallium.

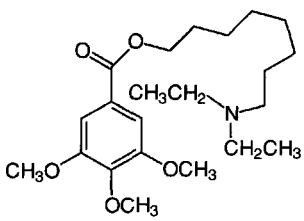
TLC *abbr. for* thin-layer chromatography.

tld a gene in *Drosophila* for **Tolloid** protein, which is required for normal dorsal development. Mutations in *tld* lead to a partial transformation of dorsal ectoderm into ventral ectoderm.

T lymphocyte *or* **T cell** any of a class of lymphocytes that undergo maturation and differentiation in thymus. They are responsible for immune reactions involving cell–cell interaction, i.e. **cell-mediated immunity**. Subsets of T lymphocytes include: (1) cytotoxic T-lymphocytes, directly reponsible *in vivo* for the death of cells identified for elimination; they include nonspecific killer cells (**NK cells**) and specific cytotoxic T-lymphocytes primed by antigen activation; (2) **helper cells**, which collaborate with **antigen-presenting cells** in the initiation of an immune response; and (3) **suppressor cells**, which down-regulate the response of helper cells.

Tm *symbol for* thulium.

TMB-8 *abbr. for* (8-diethylamino)octyl-3,4,5-trimethoxybenzoate; a Ca^{2+} antagonist that blocks intracellular Ca^{2+} channels.



TMF *abbr. for* thymocyte mitogenic factor; i.e. **interleukin 2**.

TMP *abbr. for* **1** ribosylthymine monophosphate *or* ribothymidine monophosphate, *the common names for* ribosylthymine 5′-phosphate, ribothymidine 5′-phosphate, 5′-ribothymidylyl phosphate, thymine riboside 5′-phosphate. **2** *(sometimes)* thymidine monophosphate. dTMP is recommended.

TMR spectroscopy *abbr. for* topical magnetic resonance spectroscopy.

TMS *abbr. for* **1** tetramethylsilane; a water-soluble reference substance used in nuclear magnetic resonance spectroscopy. **2** the trimethylsilyl group; the symbol Me_3Si– is preferred.

TMV *abbr. for* tobacco mosaic virus, an RNA plant virus.

Tn *abbr. for* **1** troponin. **2** transposon.

TNBS *abbr. for* 2,4,6-trinitrobenzenesulfonate; a reagent that combines readily with amino groups. It may be used either to protect these groups or to introduce a chromophore. It is removable using hydrazine.

Tn-C *abbr. for* troponin C.

TNF *abbr. for* tumour necrosis factor.

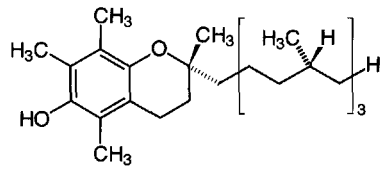
Tn-I *abbr. for* troponin I.

TNMR *or* **tnmr** *abbr. for* tritium nuclear magnetic resonance (spectroscopy).

TNS *abbr. for* 2-*p*-toluidylnaphthalene-6-sulfonate; a **fluor** used in **extrinsic fluorescence** studies of proteins.

Tn-T *abbr. for* troponin T.

tocopherol *a generic term for* di- and trimethyltocols; α-tocopherol is 5,7,8-trimethyltocol, and is active as **vitamin E**; β-tocopherol is 5,8-dimethyltocol; γ-tocopherol is 7,8-dimethyltocol; and δ-tocopherol is 8-methyltocol.



α-tocopherol

Todd, Alexander Robertus Todd, Lord Todd (1907–97), British organic chemist; Nobel Laureate in Chemistry (1957) 'for his work on nucleotides and nucleotide co-enzymes'.

T-odd phage any one of the **bacteriophages** T1, T3, T5, or T7 of *Escherichia coli*. These DNA phages share a number of morphological, biochemical, and other features that distinguish them as a group from **T-even phages**.

togavirus *or (formerly)* **arbovirus** any of a group of RNA animal viruses consisting of enveloped, icosahedral, 50–70 nm capsids with single-stranded infectious RNA (plus strand) of 4 MDa. The group contains mosquito- and tick-borne viruses causing encephalitis and yellow fever.

tolbutamide 1-butyl-3-(*p*-tolylsulfonyl)urea, *N*-[(butylamino) carbonyl]-4-methylbenzenesulfonamide; one of a number of sulfonylurea drugs, of which it is the prototype, that exert a hypoglycemic action by stimulating release of insulin from the pancreas and are used therapeutically to treat type II **diabetes mellitus**.

tolerance **1** the progressive attenuation of the response to an agent (usually a drug) whereby increasing concentrations of the agent are required to maintain the response. Underlying mechanisms confer either functional (or pharmacodynamic) tolerance, where the loss of response is due to desensitization of effector mechanisms, or metabolic (or pharmacokinetic) tolerance, whereby elimination of the agent is accelerated usually by induction of catabolic enzymes or other inactivating mechanism. **2** the ability of an organism to grow and thrive in an unfavourable environment. **3** an allowable deviation from a standard. **4 immunological tolerance**.

tolerogen an antigen that, in given circumstances, induces **immunological tolerance** when administered to an animal. Tolerogens may, when presented in different circumstances, induce an immune response. —**tolerogenic** *adj.*

Toll a developmental protein in *Drosophila melanogaster*, the product of *toll* gene, that is required for embryonic dorsal–ventral polarity. It is a type I transmembrane signalling receptor protein with a **leucine-rich repeat** segment. Precursor: database code TOLL_DROME, 1097 amino acids (124.51 kDa).

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tolloid a developmental protein in *Drosophila melanogaster* encoded by the ***tld*** gene; it is a member of the **astatin** subfamily of metalloproteinases. Database code TLD_DROME, 1057 amino acids (120.44 kDa).

tomography a radiographic technique that can image a thin plane or section of a body. An X-ray beam is focused on an area of a body, the beam is then rotated, and successive images are stored and subsequently analysed by computer (**computer-assisted tomography**, or CAT scanning). **Positron emission tomography** (or PET scanning) involves the detection of X-rays emitted from radionuclides that decay by positron emission and are located within the patient's body, e.g. from ^{15}O (**oxygen-15**) after administration of $H_2{}^{15}O$.

ton **1** *or (esp. US)* **long ton** a unit of mass equal to 2240 **pounds** avoirdupois (1016.05 kg). **2** *or (esp. US)* **short ton** *or* **net ton** a unit of mass equal to 2000 pounds avoirdupois (907.18 kg). **3** metric ton; *see* **tonne**.

tone **1** *(in physiology) or* **tonus** the state of sustained partial tension adopted by muscles in order to maintain posture, etc. It is brought about by the contraction of only a certain proportion of the muscle fibres at any given time. **2** *(in clinical medicine)* the state or degree of firmness of a muscle on palpation.

tonicity **1** the **osmotic pressure** of a solution; often used in the sense of the ratio of the osmotic pressure of a solution to that of a given reference solution. **2** (of a muscle) the condition of possessing **tone** or tension. *See also* **hypertonic**, **hypotonic**, **isotonic**.

tonin EC 3.4.21.35; *other names*: esterase 1; S2 kallikrein; RGK-2; RSKG-5; an endopeptidase, present in several rat tissues, that can cleave angiotensinogen and angiotensin-tetradecapeptide renin substrate to produce angiotensin II directly. It also acts on the Phe-|-His bond of angiotensin I to form angiotensin II. It is a trypsin- and chymotrypsin-like serine protease. Example (precursor) from rat: database code KLK2_RAT, 259 amino acids (28.22 kDa).

tonne *or* **metric ton** *symbol*: t; a unit of mass equal to 10^3 kg. 1 tonne = 0.984 207 UK ton or 1.102 31 short (US) tons.

tonometer **1** an apparatus, usually a closed glass vessel, used to equilibrate a liquid, especially blood, with a particular gas of known partial pressure. When equilibrium is established the phases are separated and the gas in question determined in both phases. **2** a device for measuring vapour pressure.

tonus *an alternative term for* **tone** (def. 1).

tooth-lid factor *a name originally given to* **epidermal growth factor**.

top+ *a variant form of* **topo+** (before a vowel).

TOPA *abbr. for* 3,4,6-trioxyphenylalanine; 6-hydroxydopa. *See also* **TOPA-quinone**.

TOPA-quinone 6-hydroxydopa quinone; the covalently bound redox prosthetic group of bovine plasma amine oxidase and some other copper-containing oxidases.

topical relating to a particular place or part of the body; local; (of a medicament, nutrient, etc.) applied locally rather than systemically. —**topically** *adv.*

topical magnetic resonance spectroscopy *abbr.*: TMR spectroscopy; a method for obtaining high-resolution **nuclear magnetic resonance** spectra from a selected place in a larger specimen (e.g. a specific organ of a living body). The sensitive volume is generated by superimposing high-order magnetic field gradients onto the main magnetic field of the spectrometer in such a manner as to define a central region of uniform field and adjustable size, surrounded by rapidly changing fields. Signals may be detected from individual nuclei, and the signals can be attributed to specific metabolites, enabling measurement of the level of these metabolites *in situ*.

topo+ *or (before a vowel)* **top+** *comb. form* denoting place or region.

topochemical **1** of, or pertaining to **topochemistry**. **2** of, pertaining to, or constituting a locally confined chemical reaction. **3** describing a combined tactile and chemical sense in some animals that is important in the perception of odours in relation to track or position.

topochemistry the characteristic chemical activity of a **topomer**.

topogenesis *an alternative term for* **morphogenesis**, especially in regard to biomolecular structures. —**topogenic** *adj.*

topogenic sequence any part of the sequence of a nascent polypeptide that is involved in getting the mature protein to its proper position in the cell. *See* (e.g.) **mannose 6-phosphate**, **signal peptide**.

topogenic signal any feature of the structure of a macromolecule that directs it to a particular organelle in a cell. The term comprehends **topogenic sequence**.

topography **1** the science and practice of describing the arrangement in space of shapes and surfaces, and of components in relation to one another. **2** the detailed description, or representation on a map, diagram, etc., of the surface features of a three-dimensional object, or part of one, with reference to the underlying structure. *Compare* **topology**. —**topographic** *or* **topographical** *adj.*; **topographically** *adv.*

topoinhibition the inhibition of a cellular process by an action at the cell membrane, especially through contact with, or proximity to, other cells.

topoisomer *or* **topological isomer** any of two or more **isomers** of a macrocyclic molecule, or system of two or more macrocyclic molecules or molecular subunits, that differ in the degree of knotting of a loop or the degree of interlocking of rings. Topoisomers of a given molecule, or system of molecules, display the same connectivity, bond orders, and configurations but can be interconverted only by breaking and reforming a covalent bond; they have different **linking numbers**. *Compare* **topomer**. —**topoisomeric** *adj.*; **topoisomerism** *n.*

topoisomerase *see* **DNA topoisomerase**.

topological bond the force equivalent to a chemical bond that may be conceived as holding together any two interlocked rings of a catenated molecular structure or two loops of a knot in a cyclic molecule. Such a bond is the property not of a pair of atoms but of the complete molecule, the strength of the union being that of the weakest chemical bond in the entire structure.

topological isomer *an older name for* **topoisomer**.

topological isomerism *an alternative term for* topoisomerism; *see* **topoisomer**.

topological winding number *see* **supercoil**.

topology **1** *(in molecular biology)* the study of deformability and deformation of structures, including macromolecules. The basic concept is founded on whether a particular figure or surface can be continuously deformed without rupture and remaking of, e.g., a chemical bond. **2** *(in botany)* the study of localities where plants are found. **3** *(in mathematics)* the branch of geometry that deals with general types of shape rather than with particular shapes and sizes; the study of relationships that remain invariant under one-to-one transformation. *Compare* **topography**. —**topological** *or* **topologic** *adj.*; **topologically** *adv.*

topomer any of two or more **conformers** of a macromolecule that have differing **topography** (def. 2). Any topomer (or its exact mirror image) is characterized by a unique set of interactions between any two residues of the complete sequence of the macromolecule. *Compare* **topoisomer**.

topotactic describing a chemical reaction in which the product has an ordered geometric relationship to the reactant.

top yeast *see* **bottom yeast**.

toroid **1** *an alternative term for* **torus**. **2** the solid enclosed by a torus. —**toroidal** *adj.*

torr *symbol*: torr; a non-SI unit of pressure, used especially in connection with low pressures. It is defined as equal to 1/760 of an atmosphere; i.e. 1 torr = 101 325/760 Pa = 133.322 Pa. Its use is now discouraged, in favour of the **pascal**. [After Evangelista Torricelli (1608–47), Italian physicist.]

torsion **1** the twisting of something about an axis by the appli-

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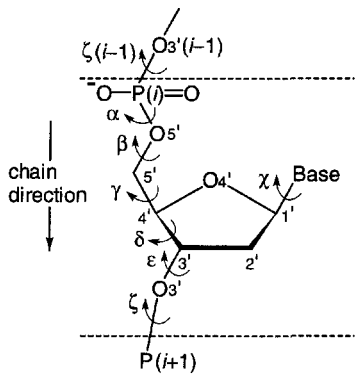
cation of equal and opposite rotational forces acting in parallel planes. **2** the twist so produced. —**torsional** *adj.*

torsion angle *symbol*: θ *or* ω; consider an assembly of attached atoms represented by the generalized partial structure X–A–B–Y where neither X nor Y is collinear with A and B: then the torsion angle is the smaller angle subtended by the bonds X–A and Y–B in a plane projection obtained by viewing the assembly along the axis A–B from either direction. The angle is considered positive or negative according as the bond to the atom nearest the viewer, X or Y, requires to be rotated to the right or left, respectively, for its direction to coincide with that of the bond to the furthermost atom, Y or X. The multiplicity of the bonding of the various atoms is not relevant. A torsion angle may similarly be defined for a partial structure X–A–Z–B–Y where Z represents one or more additional atoms and A, Z, and B are collinear. The torsion angles for the backbone of a polypeptide chain are symbolized as follows: that for rotation about the N–C^{α} bond is denoted by ϕ; that for rotation about the C^{α}-C′ bond is denoted by ψ; that for rotation about the C′–N bond is denoted by ω. The torsion angles for the backbone of a polynucleotide chain are as shown below. *See also* **conformation**, **Ramachandran plot**, **tight turn**.



designation of torsion angles for polynucleotides

torsion balance an instrument, used for the rapid weighing of small amounts of substances, in which the sample is balanced by the torsion of a wire and the amount of torsion that has to be applied to restore balance is indicated as a scale calibrated in units of mass.

torso a gene for a tyrosine kinase (EC 2.7.1.112) receptor in *Drosophila melanogaster*. The receptor is a type I membrane glycoprotein and is involved in the determination of anterior and posterior structures in the embryo. Precursor: database code KTOR_DROME, 923 amino acids (105.04 kDa).

torulin *an obsolete name for* extracts of yeast that cure polyneuritis in pigeons fed on a diet of polished rice, no doubt due to the vitamin B_1 content of yeast extract.

torus (*pl.* **tori**) a shape generated by rotating a circle or disk about an axis that is displaced outside the diameter of the circle or disk, but in the same plane; i.e. shaped like a ring doughnut (donut). *See also* **toroid**. —**toric** *adj.*

Tos *symbol for* the tosyl group.

tosyl *symbol*: Tos; *a trivial name for* the toluene-4-sulfonyl group, $CH_3–C_6H_4–SO_2–$, with which amino groups may be modified by allowing them to react with *p*-toluenesulfonyl chloride. *Compare* **pipsyl**.

total body water *abbr.*: TBW; *see* **body water**.

totipotent (of a cell) having the potentiality to develop in any of the directions inherently possible, given its particular genetic constitution, and thus to form a new organism or to regenerate any part of an organism.

toxic **1** poisonous. **2** of, relating to, or caused by a **toxin** or poison.

toxicity **1** the quality or state of being poisonous or toxic. **2** the relative degree of being poisonous or toxic; the potency of a **toxin**.

toxicogenic *an alternative term for* **toxigenic**.

toxicology the science dealing with the effects of poisons on living organisms. The term is sometimes restricted to the effects of synthetic poisons and the term **toxinology** used when dealing with naturally occurring poisons.

toxify to poison; to render poisonous. —**toxification** *n.*

toxigenic *or* **toxicogenic** *or* **toxinogenic** (especially of bacteria and fungi) producing toxin.

toxin any of various specific poisonous substances that are formed biologically. Not all such poisons are so termed, their classification as toxins being somewhat arbitrary and tending to vary with the discipline concerned; furthermore, the term is sometimes extended to include synthetic poisonous substances. Various types of toxin may be designated according to the source of the toxin, e.g. **endotoxin**, **exotoxin**, **mycotoxin**, **phycotoxin**, **phytotoxin**, and **zootoxin**, or according to the specific or prime site of action of the toxin, e.g. **hepatotoxin** and **neurotoxin**.

toxinogenic *an alternative term for* **toxigenic**.

toxinology *see* **toxicology**.

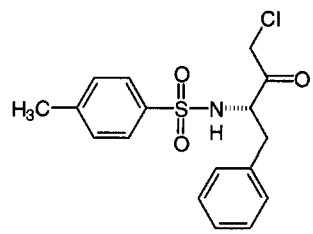
toxoid an **exotoxin** that has been modified (e.g. by formalin treatment) so that its toxicity has been lost while its antigenicity (both immunogenicity and reactivity) is retained.

toxophore a term introduced by **Ehrlich** to denote the specific chemical group in a toxin molecule that is responsible for its toxic effect. Unlike the **haptophore**, it is destroyed on conversion of the toxin to a **toxoid**.

TP *abbr. for* thymopoietin.

TPA *abbr. for* tissue-type plasminogen activator; *see* **plasminogen activator**.

TPCK *abbr. for* L-(1-tosylamido-2-phenyl)ethylchloromethyl ketone; a modifying reagent for histidine residues.



TPI *(formerly) abbr. for* **1** triphosphoinositide; use PtdInsP_2 instead (PIP_2 is also used). **2** phosphatidylinositol 4,5-bisphosphate; use PtdIns-4,5-P_2 instead. *See* **phosphoinositide**.

TPN *abbr. for* triphosphopyridine nucleotide; obsolete, use **NADP⁺**.

TPNH *abbr. for* reduced triphosphopyridine nucleotide; obsolete, use **NADPH**.

TPP *abbr. for* thiamine diphosphate (*formerly* thiamin pyrophosphate); *see* **vitamin B_1**.

TPR *abbr. for* tetratricosapeptide repeat.

tpr-met an oncogene formed by the translocation of the *tpr* (translocated promoter) locus of chromosome 1 and *MET* (the gene for **hepatocyte growth factor receptor**).

tracee *(in tracer kinetics)* the non-radioactive compound of which the tracer is the radioactive equivalent; coined to represent unambiguously what has been variously called **stable material**, **mother substance**, etc. *Compare* **compartment**.

trace element *or* **microelement** any element that is present in the body of an organism at relatively minute concentrations (often arbitrarily defined as <0.005%), and consequently is required in the organism's diet in extremely small amounts. In higher animals the most important trace elements include:

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iron, zinc, copper, manganese, iodine, cobalt, molybdenum, selenium, and chromium. The extended list includes lead, arsenic, antimony, nickel, bromine, fluorine, boron, silicon, aluminium, silver, cadmium, bismuth, mercury, vanadium, titanium, indium, barium, strontium, and lithium. The term may be extended to cover elements of primarily toxicological interest.

trace metal any **trace element** that is a metal.

tracer an element or compound containing atoms that can be distinguished from their normal counterparts by physical means, e.g. by virtue of their radioactivity, mass spectrum, colour, etc. Tracers are used in biochemistry for following the metabolic pathways of substances in an organism, cell, or cell-free system.

track an individual lane resolving the components of a single sample on a slab electrophoresis gel.

tracking dye a dye that is added to a sample on an electrophoresis gel to be the fastest component and thus to indicate visually how far the samples have run at any instant in time.

tragacanth **1** any of various thorny leguminous shrubs of the genus *Astragalus*. **2** a gum obtained especially from *A. gummifer* and used extensively in commerce, including pharmacology. It is a complex mixture of polysaccharides, including D-galacturonic acid, D-xylose, L-fucose, and D-galactose.

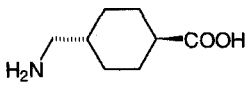
trailer sequence a sequence following the termination signal at the 3′ end of **messenger RNA**.

trait any observable, phenotypic feature of a developing or developed individual.

TRAM *or* **TRAM protein** *abbr. for* translocating chain associating membrane protein; a transmembrane protein that spans the **rough endoplasmic reticulum** of mammalian cells and plays a role in the translocation of nascent proteins destined for export from the endoplasmic reticulum. Example from *Canis familiaris*: database code TRAM_CANFA, 373 amino acids (43.03 kDa).

TRAMP *abbr. for* tyrosine-rich acidic matrix protein; *other names*: 22 kDa extracellular matrix protein; dermatopontin; a protein of the extracellular matrix that may have various binding and adhesion functions. Example from *Bos taurus*: database code DERM_BOVIN, 183 amino acids (21.99 kDa).

tranexamic acid *trans*-4-(aminomethyl)cyclohexanecarboxylic acid; a compound that inhibits binding of plasminogen and plasmin to fibrin thereby inhibiting fibrinolysis.



trans- *or (sometimes before s-)* **tran-** *comb. form* denoting across, beyond, on the other side, transverse; transfer, interchange. *See also* ***trans*-acting**.

trans- *abbr.: t-; prefix (in chemical nomenclature)* denoting a *trans*-isomer; *see* ***cis–trans* isomerism**.

***trans*-acting** describing a regulatory genetic element whose effects are insensitive to its position. Examples include the genes for bacterial repressors. *Compare* ***cis*-acting**.

***trans*-activation** gene activation by means of a ***trans*-acting** mechanism.

transacylase *an older name for* **acyltransferase**.

transaldolase EC 2.2.1.2; *other names*: dihydroxyacetone transferase, glyceronetransferase; an enzyme of the pentose phosphate pathway that catalyses the transfer of a 3-carbon glycerone moiety from sedoheptulose 7-phosphate to glyceraldehyde 3-phosphate forming erythrose 4-phosphate and fructose 6-phosphate. It has a broad substrate specificity. Example from human: database code TAL1_HUMAN, 336 amino acids (37.59 kDa).

transamidation a chemical reaction in which the amino group of an amide is exchanged for another amino group, i.e.:

$$R\text{–}CO\text{–}NHA + BNH_2 = R\text{–}CO\text{–}NHB + ANH_2.$$

Transamidation is catalysed by such proteolytic enzymes as **trypsin**, **chymotrypsin**, **papain**, and **subtilisin**.

transamidination a chemical reaction, catalysed by a transamidinase (aminotransferase) enzyme of sub-subclass EC 2.1.4, in which the amidino moiety of arginine is reversibly transferred to an amino group to form a different guanidino compound. An example is **glycine amidinotransferase**.

transaminase *an alternative name for* **aminotransferase**. *See also* **alanine transaminase**, **aspartate transaminase**, **transamination**.

transamination a chemical reaction, catalysed by any **aminotransferase** (transaminase) enzyme, in which the α-amino group of one amino acid is transferred to the α-carbon atom of an α-oxo acid. As a result, the α-oxo acid is transformed into an amino acid, and the amino acid that donated the amino group is converted to the corresponding α-oxo acid:

$$R'\text{–}CH(NH_2)\text{–}CO_2H + R''\text{–}CO\text{–}CO_2H = R'\text{–}CO\text{–}CO_2H + R''\text{–}CH(NH_2)\text{–}CO_2H$$

Transamination plays an important role in the catabolism of amino acids, in which the amino group is eventually or directly transferred to oxaloacetate (to form aspartate) or to α-oxoglutarate (to form glutamate). If transferred to aspartate, the amino group enters the **urea cycle** at the argininosuccinate step; if transferred to glutamate, the amino group is removed by glutamate dehydrogenase, yielding ammonia, which then enters the urea cycle. Transamination is also involved in *amino-acid synthesis*. *Pyridoxal phosphate is an important* coenzyme of aminotransferases. Transamination was discovered by the Russian biochemists Alexander Evseyevich Braunstein (1902–86) and Maria Grigorievna Kritzmann (1904–71).

transbilayer signifying across or through the membrane **lipid bilayer**, as in **transbilayer distribution**, transbilayer movement.

transbilayer distribution the distribution of various components between the two leaflets of a membrane lipid bilayer, but often referring specifically to lipids. In the plasma membrane this distribution is asymmetric, particularly with regard to phospholipids: phosphatidylcholine and sphingomyelin are relatively enriched in the outer leaflet, and phosphatidylethanolamine and phosphatidylserine are more predominant in the inner leaflet (i.e. the cytoplasmic face).

transcarboxylase **1** methylmalonyl-CoA carboxyltransferase; EC 2.1.3.1; *systematic name*: (*S*)-2-methyl-3-oxopropanoyl-CoA:pyruvate carboxyltransferase; a biotinyl-protein, containing cobalt and zinc, that is present in prokaryotes and catalyses the transfer of a carboxyl group from methylmalonyl-CoA [(*S*)-2-methyl-3-oxopropanoyl-CoA] to pyruvate forming oxaloacetate and propanoyl-CoA. **2** a component of the prokaryote form of **acetyl-CoA carboxylase** that transfers the carboxyl group from *N*-carboxybiotin to acetyl-CoA.

transcarboxylation the transfer of a carboxyl group from one compound to another, e.g. as catalysed by a **transcarboxylase**.

transconjugant a bacterial cell that has received genetic material from another bacterium by **conjugation**. A transconjugant should be referred to as a **recombinant** only if the transferred genetic material has been inserted into a pre-existing **replicon** in the recipient. If the transferred material is perpetuated *per se* as a plasmid, then the cell is called a **plasmid transconjugant**. If such material is not a plasmid and does not become a resident replicon, it will fail to replicate; the bacterium will be called an **abortive transconjugant**.

transcortin a specific plasma α_1-globulin, M_r 52 000, that binds **cortisol** at one binding site and serves to transport the hormone. It also binds corticosterone and certain other steroid hormones; aldosterone is bound only weakly. Transcortin is synthesized in the liver. The normal serum concentration of transcortin is 3–4 mg dL^{-1}; saturation occurs at a cortisol serum concentration of about 28 μg dL^{-1}, other cortisol being

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less tightly bound to albumin or (about 5%) unbound. *Other names*: corticosteroid-binding globulin; corticosteroid-binding protein; cortisol-binding globulin (*abbr.*: CBG); cortisol-binding protein.

transcribe 1 to copy. 2 to use DNA as a template for the synthesis of mRNA, or, in some cases (e.g. as in retrovirus infection), to synthesize DNA from an RNA template. *See* **transcription**.

transcribing strand *an alternative name for* **noncoding strand** (of duplex DNA).

transcript the product of a **transcription** process; the **primary transcript** is the immediate product of a polymerase engaged in transcription (e.g. RNA polymerase).

transcriptase *an alternative name for* **DNA-dependent RNA polymerase**.

transcription the synthesis of either RNA on a template of DNA or DNA on a template of RNA. The latter is important in the replication of **retroviruses** by the enzyme **reverse transcriptase** and will not be further described here. Concerning the transcription of double-stranded DNA the older literature is confusing in terms of the use of the word transcription until the discovery of transfer RNA in 1956 when it became clear that RNA was an intermediary in the transfer of information contained in the base sequence of DNA to the polypeptide chain of protein. In the transcription of double-stranded DNA the RNA is formed on a template comprising only one strand, which we will name the transcribed strand. This is also called the antisense strand since the mRNA is termed the sense strand. Similarly the transcribed strand may also be named the noncoding strand, the coding strand having the same base sequence as the mRNA. Transcription involves many steps. (1) The region of DNA to be transcribed must be unwound approximately one turn to form an open loop to allow the transcribed strand to form a DNA–RNA double helix with the 3′ end of the newly synthesized RNA. (2) The mRNA is transcribed by **RNA polymerase** utilizing nucleoside triphosphates as substrates. The enzyme binds to the **promoter**, which is a region of DNA on the nontranscribed strand that has a characteristic base sequence (e.g. **TATA box**). Promoters are mostly located upstream of the start of transcription. However, in the case of eukaryotic RNA polymerase III, the promoter may sometimes be located downstream of the start point. There are substantial differences between prokaryotic systems and eukaryotic systems for the regulation of transcription. In prokaryotes, for transcription to proceed, a complex must be formed on the double-stranded DNA helix with the promoter and an accessory factor, **sigma factor**. In eukaryotes, an extensive and complex system of **transcription factors** regulates the process. While prokaryotes appear to utilize only a single RNA polymerase, eukaryotes possess three RNA polymerases, which are responsible for transcribing the various specific types of RNA. Thus RNA polymerase I is located in the nucleolus and is responsible for the synthesis of ribosomal RNA. This polymerase accounts for by far the greatest quantity of RNA synthesized. RNA polymerase II is situated in the **nucleoplasm** and is responsible for the synthesis of heterogeneous nuclear RNA, for **primary transcript** from which messenger RNA is formed. This polymerase is thus instrumental in determining the nature of the protein profile of the cell. RNA polymerase III is also in the nucleoplasm and synthesizes transfer RNA. In so far as eukaryotes are concerned, what follows refers mainly to the activity of RNA polymerase II. (3) As the enzyme advances along the DNA template the DNA unwinds ahead of the growing RNA and rewinds behind it thereby stripping the newly synthesized RNA from the transcribed strand of the DNA. The origin of the energy requirements for this movement is not known at present. Eventually the movement is terminated by specific sequences in the transcribed DNA strand. In some cases **rho protein** plays a part in termination. (4) **Transcription factors**, which may be ***cis*-acting** or ***trans*-acting**, control transcription. In prokaryotes the control of transcription is induced by the environment and changes are very rapid since transcription and translation are tightly coupled. In eukaryotes such changes are slower. The activity of eukaryotic transcription factors is enhanced by proteins called **enhancers**, which although lacking promoter activity may nevertheless exert their influence over distances of several thousand base pairs. They may be **upstream**, **downstream**, or even in the midst of a transcribed gene. They may also be tissue specific. In the case of eukaryotes where the gene is split by **introns** the entire gene is transcribed and the introns are subsequently excised from the primary transcript by splicing.

transcriptional repressor any **transcription factor** (usually bacterial) that down-regulates gene expression by binding to an **operator**.

transcriptional unit the segment of DNA within which the **transcription** occurs that eventually leads to RNA formation. *Compare* **cistron**, **gene**.

transcription factor *abbr.*: TF; any protein required to initiate or regulate **transcription**; the term includes **enhancers** as well as the general transcription factors. Transcription factors bind to DNA sequence elements upstream of the **start point** and thus participate in the formation of the complex that includes RNA polymerase and initiates transcription. *See, e.g.* **NF-KB**, **Oct**, **TFII**, **TFIII**.

transcytosis the transport of molecules across a cell, especially across a **polarized cell**, such as an intestinal epithelial cell, which has a basolateral and an apical surface each with its own defined composition, which thus provides a spatially orientated transport system. The molecules undergoing transcytosis are usually contained within vesicles. One example is the absorption of maternal antibodies from the gut in newborn animals. The antibodies are taken into epithelial cells by endocytosis at the apical surface, and are transcytosed through the cell before being exocytosed at the basal surface into the blood. Transcytosis also occurs in thyroid cells: following endocytosis of thyroglobulin from the thyroid follicle, the thyroglobulin is transported across the cell in vesicles with concomitant proteolysis, with release of thyroid hormone into a blood capillary at the opposite face of the cell (*see* **thyroid gland**). —**transcytotic** *adj.*; **transcytose** *vb.*

transdeamination *a former term for* the coupling of a transamidation reaction and the dehydrogenation of L-glutamate whereby an amino group of an amino acid is transferred to α-oxoglutarate by a transaminase enzyme and the resulting L-glutamate is dehydrogenated to yield α-oxoglutarate, ammonia, and a reduced coenzyme molecule.

***trans*-dominant mutation** a mutation in a regulatory gene that can control the expression of a structural gene on another chromosome.

transducer any device that converts a quantity of energy from one form into another.

transducin *abbr.*: G_T *or* G_t; a heterotrimeric **G-protein** of the retina, and a component in the visual transduction pathway. In the vertebrate light response, inactive heterotrimeric transducin with bound GDP ($G_{t\alpha\beta\gamma}$·GDP) binds the photoactivated rhodopsin, metarhodopsin II, and releases GDP. GTP then binds to the α subunit, which then separates from both the receptor and the $\beta\gamma$ heterodimer. $G_{t\alpha}$ then activates cyclic GMP phosphodiesterase, and the resulting fall in cyclic GMP concentration closes cyclic GMP-gated cation channels and hyperpolarizes the retinal rod cell, generating the nerve impulse. Examples from human, α_2 subunit: database code GBT2_HUMAN, 353 amino acids (40.04 kDa); β_2 subunit: database code GBB2_HUMAN, 340 amino acids (37.33 kDa); γ subunit: database code GBG1_HUMAN, 73 amino acids (8.36 kDa).

transduction 1 *(in microbiology)* the transfer of genetic information to a bacterium from a bacteriophage or between bacterial or yeast cells mediated by a phage vector. In **generalized transduction** any of the donor genes may be transduced, whereas in **specialized transduction**, i.e. by a **lysogenic** bacterio-

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phage, only those genes at one of the ends of the prophage can be transduced. **Abortive transduction** occurs when phage DNA is not incorporated into the bacterial genome, but can nevertheless be transmitted in the phage to one of the daughter cells. **2** *(in biochemistry)* the activation of an intracellular effector pathway as a result of receptor activation by an extracellular signal. *See also* **second messenger**, **signal transduction**.

transesterification a chemical reaction in which the alcohol moiety of an ester is exchanged for another alcohol:

$$R\text{–}CO\text{–}OA + BOH = R\text{–}CO\text{–}OB + AOH$$

It is catalysed by such proteolytic enzymes as trypsin, chymotrypsin, papain, and subtilisin, and by esterases.

transfection originally the process of infection of competent bacterial cells by free bacteriophage or plasmid nucleic acid that results in the subsequent production of normal bacteriophage or plasmids in the infected bacterial cell. It has come to mean the process of bringing about genetic alteration of any cell or organism using recombinant DNA technology.

transferase an enzyme that catalyses the transfer of a group – e.g. the methyl group, glycosyl group, acyl group, phosphorus-containing, or other groups – from one compound (generally regarded as the donor) to another compound (generally regarded as the acceptor). Transferases, of which there are many, are EC class 2 enzymes.

transference number *or* **transport number** *symbol*: t; the fraction of the current being carried by a given type of ion when an electric current is passing through an electrolytic solution.

transfer factor a **lymphokine** extractable from leukocytes and thought to transfer the ability to elicit a **delayed hypersensitivity** reaction from one person or animal to another.

transfer gene any gene carried by a **conjugative plasmid** that is responsible for the donor phenotype.

transfer membrane a membrane used with **blotting** techniques in recombinant DNA technology or protein studies. Molecules are transferred from an electrophoretic gel to the transfer membrane either by capillary attraction or by using an electric potential (**electroelution**). Transfer membranes may be of three types: (1) nitrocellulose – mixed esters of cellulose acetate and cellulose nitrate; high cellulose nitrate improves binding of biomolecules while a low percentage of cellulose acetate improves handling properties; nucleic acids can be fixed to nitrocellulose membranes by baking; (2) nylon, which is physically more robust and reusable, and to which nucleic acids can be fixed by exposure to ultraviolet light; or (3) polyvinylidene-based membranes.

transfer potential *another name for* **group transfer potential**.

transfer reaction *another name for* **group transfer reaction**.

transferrin any of a class of single-chain (76–81 kDa), metal-binding glycoproteins, widely distributed in physiological fluids and cells of vertebrates, with the characteristic property of a stringent association of their metal-combining properties with an anion-binding requirement; iron-binding transport proteins, that bind two Fe^{3+} in association with bicarbonate (or other anion). They are monomers with internal homology. An essential component in cell culture media, transporting iron into cells through the **transferrin receptor**. The transferrin family includes proteins such as **lactoferrin**, **melanotransferrin** (with electrophoretic polymorphisms), ovotransferrin (*see* **conalbumin**), and **serotransferrin**. Examples: serotransferrin (*other names*: siderophilin; β-1-metal binding globulin) from human (precursors): database code TRFE_HUMAN, 698 amino acids (76.96 kDa); transferrin precursor from *Xenopus laevis*: database code TRFE_XENLA, 717 amino acids (79.53 kDa).

transferrinjection a method of gene transfer in which DNA complexed to transferrin–polycation conjugates is introduced into cells by receptor-mediated endocytosis.

transferrin receptor a transmembrane protein involved in the cellular uptake of iron, bound to transferrin, which binds to the receptor and is taken into the cell via receptor-mediated endocytosis. Structurally it is a dimer (a soluble serum form is a monomer lacking amino acids 1–100), the extracellular domains of the two chains being linked by a disulfide bridge, and carrying the glycan moieties. The intracellular domain is phosphorylated and palmitoylated, i.e. acylated with a palmitoyl group by a process analogous to **myristoylation**. Synthesis of the receptor is regulated by binding of aconitase to mRNA when intracellular iron concentrations are low, stimulating receptor synthesis, possibly by stabilizing the mRNA. Example from human: database code TRSR_HUMAN, 760 amino acids (84.81 kDa).

transfer RNA *abbr.*: tRNA; any of a class of relatively small **RNA** molecules each of which mediates the insertion of an amino acid at the correct point in the sequence of a nascent polypeptide during protein synthesis. Crick predicted that the amino acids would not directly interact with the triplet nucleotide bases comprising the codons in mRNA but that interaction would involve a small nucleic acid to which the 20 different amino acids would be attached. The discovery of such an RNA molecule in the soluble cell extract required for the synthesis of protein in an *in vitro* system derived from rat liver by Hoagland was greeted as confirmation of Crick's hypothesis. Since the RNA was present in the soluble (non-particulate) extract it was called at first **soluble RNA** or S-RNA. With 73–93 nucleotides, tRNA ($M_r \approx 25\,000$) was rather larger than had been expected for adaptor RNA (*see* **adaptor hypothesis**). It was soon shown that the amino-acid residue was attached by ester link to the 3′ terminal of tRNA at either the 2′- or 3′-OH on the ribose. Specific tRNA molecules are found for the various amino acids, but in all cases the amino acid is attached to the adenosine of a CCA sequence at the 3′ end of the tRNA molecule. The amino acids are attached to tRNA by specific amino acid-tRNA ligases, which first catalyse a reaction between the amino acid and ATP to form an aminoacyl-adenylate, and then transfer the aminoacyl group to the tRNA. Each tRNA possesses an **anticodon** of three nucleotides that base pairs in an antiparallel fashion with the codons of mRNA. While there are 61 sense codons there are only about 41 different tRNAs in the cytopasm and even fewer in mitochondria due to flexibility in the base pairing between codon and anticodon (*see* **wobble hypothesis**). When the sequence of tRNA for phenylalanine was determined by Holley it could be shown that the secondary structure contained three loops reminiscent of a clover-leaf if the maximum amount of base pairing was allowed for. This involved about half the residues. The anticodon was predicted to be on a loop lacking base pairing. This was shown to be true, it being located on the middle of the three loops. The few tertiary structures that have been determined for tRNAs have supported the clover-leaf structure. It has been predicted that **initiator transfer RNA** would have a structure that differentiated it from the other tRNAs but this has not been firmly established. tRNA is characterized by the presence of many unusual **minor bases** the function of which has not been completely established. *Other names*: acceptor RNA; amino-acid-accepting RNA; *(formerly)* soluble RNA (*abbr.*: S-RNA *or* sRNA). *See also* **suppressor tRNA**.

transform **1** to bring about **transformation**. **2** *(in mathematics)* **a** a process for deriving one mathematical entity from another. **b** the transformed entity itself.

transformant a bacterial cell that has undergone **transformation** (def. 1), i.e. one that contains integrated donor genes that can be detected by plating on media selective for some or all of the donor genes.

transformation **1** *or* **genetic transformation** the intraspecific and interspecific (between members of different but related species) transfer of genetic information by means of 'naked' extracellular DNA in bacteria. In transformation, in contrast to **transduction**, the DNA not integrated into the recipient's genome cannot function and manifest its genetic information phenotypically. **2** characteristic and inherited changes produced in cells in culture when they have been treated with cer-

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tain viruses (which may be DNA- or RNA-containing), or with chemical carcinogens, or with X-rays, or when they have been subjected to genetic modification by DNA technology. In animal cells, these changes include certain specific alterations in morphology (especially of the nucleus) and stainability, and the cells usually show a loss of **contact inhibition** and have a capacity to give rise to neoplastic growth on injection into animals. The term is usually extended to refer to corresponding changes occurring in cells *in vivo*. **3** *or* **blast transformation** *or* **lymphocyte transformation** the morphological and other changes that occur in both B and T lymphocytes when they are cultured in the presence of an antigen to which they are primed, or that occur nonspecifically in B lymphocytes when they are exposed to a mitogen (e.g. certain lectins). The lymphocytes increase in size and develop a basophilic ribosome-rich cytoplasm, a prominent nucleolus, and a paler-staining nucleus. After about three days these cells resemble **blast cells**. **4** the alteration produced in certain specific hormone-receptor proteins, present in the extranuclear region of hormone-responsive cells, when the hormone binds to them. This alteration is accompanied by the migration of the hormone–receptor complexes to the nucleus. **5** *or* **nuclear transformation** (of an atomic nucleus) the change of one **nuclide** to another.

transforming growth factor *abbr.*: TGF; either of two types of mitogenic **cytokine**, TGFα and TGFβ. **TGFα** was isolated and purified on the basis of its ability to stimulate cell growth in soft agar. It is produced by macrophages, brain cells, and keratinocytes, and is mitogenic for fibroblasts, is angiogenic *in vivo*, and induces epithelial development. It is a glycoprotein and a member of the **epidermal growth factor** (EGF) family, interacting with the EGF receptor. TGFα comprises 50 amino acids with the following sequence (residues invariant in the EGF family are underlined): VVSFHNDCPDSHTQFCFHG-TCRFLVQEDKPACVCHSGYVGARCEHADLLA. Example from human (precursor): database code TGFA_HUMAN, 160 amino acids (16.99 kDa). **TGFβ** is a multifunctional peptide that controls proliferation, differentiation, and other functions in many cell types. It is produced by fibroblasts, platelets, monocytes, chondrocytes, and osteoblasts. A glycoprotein with EGF repeats, at least five types (TGFβ1 to TGFβ5) are known; all have 112 amino acids except TGFβ5, which has 114. They have a great many biological activities and can be mitogenic or antiproliferative depending on cell type. Platelets contain large amounts, but these proteins are also found in a variety of cell types. Example, TGFβ1 precursor (human): database code TGFA_HUMAN, 1394 amino acids (152.62 kDa); alternative splicing results in different forms in platelets and fibroblasts.

transforming growth factor receptor any of the membrane proteins that bind transforming growth factor β (TGFβ) and mediate its effects. Three types of receptor for TGFβ have been distinguished: types I and II have high affinity for TGFβ1, with lower affinity for TGFβ2; type III has high affinity for TGFβ1, 2, and 3. Types I and II have a single transmembrane domain with a cytoplasmic protein serine/threonine domain. The following examples are all from human. Type I receptor: database code KIR4_HUMAN, 503 amino acids (55.96 kDa); type II receptor: database code TGR2_HUMAN, 567 amino acids (64.54 kDa); type III receptor (has a single transmembrane domain; little cytoplasmic structure): database code TGR3_HUMAN, 849 amino acids (93.38 kDa); residues 1–16 are the signal; 17–781 extracellular domain (heavily glycosylated, 808–849 intracellular. It may present TGFβ to the signalling receptors.

transforming principle *a historical name for* the purified DNA that, when incorporated into a bacterial cell, brings about the **transformation** (def. 1) of that cell. The term was used, most famously, by Oswald Theodore Avery (1877–1955, US bacteriologist and immunologist) and colleagues in their work establishing that DNA, not protein, was responsible for genetic transformation. In a classic experiment, they used two strains of *Pneumococcus*. The first was a wild strain, known as S (for smooth) strain because of the kind of colony that it forms, that is pathogenic. The other was a mutant strain, known as R (for rough) strain, that is non-pathogenic. When mice were injected with live R strain or heat-killed S strain, they remained healthy, but when injected with a combination of live R strain and heat-killed S strain they died. These workers concluded that the live R strain could be transformed into a pathogenic strain by material from the heat-killed S strain, and were able to demonstrate that the material was DNA.

transfuse to transfer blood from one animal into the circulation of another animal, or to inject liquid into the circulation of an animal to maintain the circulating fluid volume. —**transfusion** *n.*

transgene a gene that is inserted, using cDNA technology, into the germ line in a manner that ensures its function, replication, and transmission as a normal gene. *See also* **transgenesis**, **transgenic**. —**transgenic** *adj.*

transgenesis the creation in plants or animals of a stably incorporated gene or genes derived from another cell or organism which can be passed on to successive generations.

transgenic describing an organism harbouring in its germ line a gene that has been introduced using cDNA technology (*see* **complementary DNA**). In animals, the less transgene is introduced during transient culturing of an egg or early embryo, which is then implanted into a foster mother. Introduction of the transgene may involve any of several distinct techniques: cells may be transferred from one embryo to another (to produce a **chimera**); **pluripotent** cells can be introduced into an embryo; cells infected with a retrovirus can be introduced; or cDNA can be introduced by microinjection into the pronucleus of a fertilized egg. In plants, plasmids from *Agrobacterium tumefaciens* have been widely used to produce transgenic varieties. The **Ti plasmid** is a natural vector for genetically engineering plant cells, because it can transfer its **T-DNA** to the plant genome. A number of vectors have been constructed based on this system. Expression of the introduced genes can be controlled by suitable promoters, such as the cauliflower mosaic virus promoter.

transgenomes large complexes of DNA found inside recipient cells following transfection of the latter with calcium phosphate-precipitated DNA.

transgenosis the overall phenomenon of transfer of genetic information between unrelated organisms and the subsequent expression of such information (including gene maintenance, transcription, translation, and function), especially when donor and recipient cells are widely separated by evolution (e.g. bacterial and eukaryotic cells respectively) and when the mechanisms of gene transfer and maintenance are obscure. *Compare* **transgenesis**.

transglycosylation a chemical (enzymic) reaction in which one glycosyl residue is transferred from a glycoside onto a receptor molecule so as to form a new glycosidic linkage, e.g. in the biosynthesis of polysaccharides. The process therefore involves breaking simple glycosidic linkages and reforming them into different types of glycosidic linkages. **Glycosyltransferases** are in subclass EC 2.4; also included in the term are glycosyl transfers to water and to inorganic phosphate.

transient **1** temporary, transitory, short-lived. **2** a sudden, short-lived disturbance in a system. **3** a short-lived chemical species such as an excited atom or molecule or a free radical.

transient-phase kinetics *an alternative name for* **pre-steady-state kinetics**.

***trans* isomer** *see* ***cis–trans* isomer**.

transition *(in molecular biology)* a particular type of mutation by single base-pair substitution that occurs by replacement of one purine by another purine, or one pyrimidine by another pyrimidine whether by chemical change or by substitution. *Compare* **transversion**.

transition element *or* **transition metal** any element whose atom has an incomplete d-subshell of extranuclear electrons,

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or which gives rise to a cation or cations with an incomplete d-subshell. Such elements fall into groups 3 to 11 inclusive of the IUPAC **periodic table**. (Elements of group 12, which formerly were also considered as transition elements, have complete d-subshells and are now excluded.) The first series of transition elements is in period 4 of the periodic table and comprises those of proton numbers 21 to 29 inclusive, i.e. the elements scandium, titanium, vanadium, chromium, manganese, iron, cobalt, nickel, and copper; the second series is in period 5 and comprises those of proton numbers 39 to 47 inclusive, i.e. the elements yttrium, zirconium, nobium, molybdenum, technetium, ruthenium, rhodium, palladium, and silver; the third group is in period 6 and comprises those of proton numbers 57 to 79 inclusive, i.e. the **lanthanoids** together with the elements hafnium through to gold; and the fourth series is in period 7 and contains those of proton numbers 89 to 103 inclusive, i.e. the **actinoids**, and may well be found also to contain a number of elements of proton number 104 or more that yet remain to be characterized or discovered. The lanthanoids and actinoids are designated **inner transition elements** of periods 6 and 7 respectively; their atoms also have incomplete inner f-subshells of electrons. All transition elements are metals, they often have more than one valency state, and they form many coordination complexes, which frequently are coloured.

transition state *or* **activated complex** *(in enzymology)* the state of most positive molar **Gibbs energy** through which an assembly of atoms must pass on going from the reactants of a single-step chemical reaction to the products. This is the state that occurs immediately after binding of the reactants to the enzyme's active site; it is during this time that transient bonds between reactants and enzyme are first formed, and initial electronic interactions occur. It is followed by a state in which more stable intermediates form, prior to the eventual formation of products.

transition-state theory the theory that relates the rate of an enzymic reaction to the difference in **Gibbs energy** between the **transition state** and **ground state** ($\Delta G^{\ddagger}$). If x is the ground state and $x^{\ddagger}$ the transition state, then the rate of decomposition of x is given by:

$$-\mathrm{d[x]/d}t = \nu[x^{\ddagger}] = [x](kT/h)\exp(-\Delta G^{\ddagger}/RT),$$

where ν is the vibrational frequency of the bond that is breaking, h is the Planck constant, k the Boltzmann constant, R the gas constant, and T the thermodynamic temperature.

transition temperature *symbol*: T_t; (of a membrane lipid) the surface temperature at which a heated lipid bilayer undergoes transition from one physical state (e.g. liquid crystalline) to another (liquid). *See also* **pretransition temperature**, **phase transition (of lipids)**.

transit peptide any ≈4 kDa peptide sequence at the N or C terminus (or both) of cytoplasmically synthesized precursor proteins of certain chloroplast proteins that contains the information to ensure both the specific post-translational transport of the protein into the chloroplast and its localization within the organelle. The transit peptide is removed within the chloroplast.

transit time the time taken by a coenzyme or metabolite in travelling between two enzymes. If the two enzyme reactions were infinitely fast, the overall velocity would be determined by the reciprocal of the transit time.

transketolase EC 2.2.1.1; *systematic name*: sedoheptulose-7-phosphate:D-glyceraldehyde-3-phosphate glycolaldehydetransferase; *other name*: glycolaldehyde transferase. An enzyme that catalyses the transfer of a glycolaldehyde ($HOH_2C–CHO–$) moiety from xylulose 5-phosphate to ribose 5-phosphate to form glyceraldehyde 3-phosphate and sedoheptulose 7-phosphate. A component of the pentose phosphate pathway, it requires thiamine diphosphate (TPP) as coenzyme; a glycolaldehyde–TPP intermediate is formed transiently during the reaction. It has broad substrate specificity. In clinical chemistry, the measurement of transketolase activity in a red cell hemolysate, in the presence and absence of thiamin, gives an indication of the thiamin status of the individual by revealing the degree of activation of the enzyme in the absence of thiamin, compared with the activity in the presence of optimal concentrations. Example from human (homodimer): database code TKT_HUMAN, 623 amino acids (67.72 kDa).

translation **1** *(in molecular biology)* the process by which a particular sequence of bases in messenger RNA (mRNA) determines a sequence of amino acids in the polypeptide chain being assembled during **protein and peptide biosynthesis**. One or more specific base triplets (codons) code for each of the 20 amino acids that may be incorporated into the polypeptide chain (*see* **genetic code**). Each codon of the mRNA molecule is recognized by the corresponding anticodon on the **transfer RNA** to which the amino acid is attached. The transfer RNA binds to a site on the large subunit of the **ribosome**, which is associated with the small subunit to which the mRNA is bound. The first codon (the initiation codon) in each mRNA molecule is AUG, which codes for formylmethionine (in prokaryotes and mitochondria) or methionine (in eukaryotes). The methionine or formylmethionine, or just the formyl group, is removed before the chain is completed. Completion of translation is signalled by one of three termination codons. **Release factors** effect the release of the complete polypeptide chain and the dissociation of the two subunits of the ribosome. **2** movement or displacement laterally in space without rotation or change of orientation.

translational frictional coefficient *see* **frictional coefficient**.

translocase a system catalysing translocation of a substrate across an osmotic barrier. *See* **EF-G**, **translocator**.

translocation a vectorial transfer process, e.g. of a solute across a membrane. —**translocation** *adj.*

translocator *or* **porter** **1** a system catalysing a secondary translocation reaction, i.e. one not involving primary bond exchanges between different pairs of chemical groups or the donation and acceptance of electrons. **2** any molecular group that is attached to a substrate during transport of the latter across a membrane.

translocon a translocation complex that constitutes the specific site of protein translocation across the endoplasmic reticulum. It involves the **signal recognition particle receptor**. The component proteins are known as **translocon-associated proteins** (*abbr.*: TRAP). They may be involved in ensuring retention in the endoplasmic reticulum of resident proteins. TRAP proteins form a heterotetramer of α, β, γ, and δ subunits. Examples, α from *Arabidopsis thaliana*: database code SSRA_ARATH, 253 amino acids (27.5 kDa); β from dog: database code SSRB_CANFA, 183 amino acids (20.1 kDa); γ from rat: database code SSRG_RAT, 185 amino acids (21.11 kDa); δ from rat: database code SSRD_RAT, 173 amino acids (18.98 kDa).

translucent transmitting light (or other radiation) with some scattering or diffusion. Consequently, objects cannot be clearly distinguished through translucent materials. *Compare* **transparent**. —**translucence** *or* **translucency** *n.*

transmembrane protein any protein that traverses the membrane, especially the plasma membrane. For the different types *see* **membrane protein**.

transmethylation the transfer of a methyl or methylene group, as frequently occurs in **one-carbon metabolism**. Methyltransferases are in sub-subclass EC 2.1.1, and enzymes concerned with one-carbon metabolism are in sub-subclass EC 2.1.2. *See also* **C_1 compound**, **folate coenzymes**, ***S*-adenosylmethionine**.

transmission **1** the act, process, or an instance of transmitting. **2** the proportion of radiant energy that is transmitted perpendicularly through a substance or solution; *compare* **transmittance**. **3** the delivery of a nerve stimulus across a **synapse**, e.g. by a neurotransmitter.

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transmission coefficient *(in nuclear physics)* the probability that a particle striking a nucleus penetrates it.

transmission electron microscope *abbr.*: TEM; *see* **electron microscope**.

transmission factor *an alternative name for* **transmittance**.

transmittance *or* **transmission factor** **1** *(in chemistry) symbol*: T; the ratio I/I_0, where I_0 is the intensity of electromagnetic radiation falling on a body or substance and I the intensity after transmission through it. It is a dimensionless physical quantity. **2** *(in physics) symbol*: τ; the fraction of radiant energy that, having entered an absorbing substance, reaches its far boundary. It is given by

$$\tau = \Phi_{tr}/\Phi_0 = \exp(-\kappa c l),$$

where Φ_{tr} and Φ_0 are the radiant powers of the transmitted and incident radiation, κ is the molar napierian absorption coefficient, c the speed of light in the medium, and l the path length.

transmitter-gated channel *see* **ion channel**.

transparent transmitting light with little scattering or diffusion so that objects beyond the transparent material can be clearly distinguished. The term can be used in appropriate circumstances to indicate materials allowing the passage of other electromagnetic, particulate, or sonic radiation without disturbance. *Compare* **translucent**. —**transparency** *n.*

transpeptidase **1** *(sometimes) an alternative term for* **peptidyltransferase**. **2** *(sometimes)* the enzymic activity of a number of proteinases that catalyse, apart from hydrolysis of peptide links, the replacement of one terminal amino-acid residue in a peptide by another amino acid or other suitable molecule. **3** *(sometimes)* certain aminoacyltransferase enzymes, e.g. D-glutamyl transpeptidase, D-glutamyltransferase (EC 2.3.2.1), and glutamyl transpeptidase (i.e. **γ-glutamyltransferase**, EC 2.3.2.2).

transpeptidation any of the reactions catalysed by **transpeptidases**.

transphosphoribosidase *see* **adenine phosphoribosyltransferase**.

transplantation antigen *an alternative term for* **histocompatibility antigen**.

transport the movement of a material from one place to another, especially in reference to the movement of substances around the body (e.g. in blood) or across a biological membrane, or of electrons along a series of carriers. This term implies a positive agency, in contradistinction to **passive diffusion**. *See also* **active transport**, **antiport**, **facilitated diffusion**, **symport**, **transport protein**.

transporter a membrane protein catalysing the passage of molecules from one face of a membrane to the other.

transport method *see* **transport process**.

transport number *an alternative term for* **transference number**.

transport piece *see* **secretory piece**.

transport process any process, such as sedimentation, diffusion, or electrophoresis, that is irreversible in the thermodynamic sense. The system in which such a process occurs is removed from a state of equilibrium. Such processes are of particular value in providing information about the dimensions, shapes, and masses of macromolecules.

transport protein a protein (or enzyme) that is instrumental in transporting material, often in a specific manner, across a biological membrane or within a biological fluid (e.g. blood).

transposable element *another name for* **transposon**.

transposase an enzyme that is responsible for the transposition of **transposable elements** or **transposons**. Transposases are involved in site-specific DNA recombination required for transposition in bacteria and other organisms. Example, Tn3 (*Escherichia coli* and *Klebsiella pneumoniae* transposon) transposase: database code TRA1_ECOLI, 1015 amino acids (114.40 kDa).

transpose **1** to alter the position of; to interchange or place in a different order. **2** *(in mathematics)* **a** to interchange the rows and columns of a **matrix** (def. 8). **b** the matrix resulting from interchanging the rows and columns of a given such matrix.

transposition **1** the process of transposing or the state of being transposed. **2** something that has been transposed; especially a segment of a chromosome or a piece of a DNA molecule.

transposition sequence *an alternative name for* **translocation sequence**.

transposon *or* **transposable element** a specific DNA sequence that is transferred as a unit from one **replicon** to another. Transposons were first identified as a result of work on **transposable elements** and also as spontaneous insertions in bacterial operons. The simplest transposons are referred to as **insertion sequences**. These have the designation IS followed by a number related to the sequence in which they were identified, preceded by an indication of the site of insertion followed by a double colon (thus λ::IS1 indicates an IS1 element inserted into phage lambda). Each end of the transposon is characterized by repeated sequences, due to short sequences copied from the original gene called **target repeats** or **direct repeats**, and also due to short inverted repeats that are a property of the insert. More complex transposons, called **composite transposons**, may have a central portion having a variety of markers, the central portion being flanked by IS elements that are responsible for identifying the transposon for transposition. Composite transposons have the designation Tn followed by a number. In eukaryotes, transposable elements constitute much of the **repetitive sequences** in the genome, with up to a few hundred repeat copies. They are flanked by terminal inverted sequences; the terminal sequences in each strand characteristically represent the complementary bases of the inverted sequence, i.e. TCAG.....CGTA. Some transposons move physically from one site to another, while others are replicated, with one copy remaining at the original site and a duplicate inserting elsewhere. Both mechanisms involve a **transposase** enzyme; the former requires a **resolvase** enzyme in addition.

transthyretin a thyroid-binding protein occurring in the bloodstream and having an unusual structure. The molecule is a homotetramer; each monomer comprises two four-stranded beta sheets and has the shape of a prolate ellipsoid. Two of the monomers dimerize and the dimers themselves dimerize to form a structure with an internal channel. Example (precursor) from human: database code TTHY_HUMAN, 147 amino acids (15.87 kDa).

transudate any fluid, with its solutes, that has passed through a membrane or through the interstices of a system.

transude to pass or be passed through a membrane or the interstices of a system as a **transudate**. —**transudation** *n.*

transversion the particular type of mutation by single base-pair subsitution that occurs by the insertion of a purine in a duplex nucleic acid, in place of a pyrimidine, or vice versa. *Compare* **transition**.

TRAP *abbr. for* translocon-associated protein; *see* **translocon**.

trap hypothesis **1** a proposed mechanism for the binding of proteinases by **α_2-macroglobulin** (α_2M). It is suggested that, when α_2M interacts with a proteinase, hydrolysis of one or more of its susceptible peptide bonds in its **bait region** occurs, whereupon the α_2M molecule undergoes a conformational change that physically entraps the proteinase molecule, thus sterically hindering reaction between the proteinase and other large substrate molecules. **2** *see* **methyltetrahydrofolate trap hypothesis**.

Trasylol *a proprietary name for* **aprotinin**.

TRE *abbr. for* **1** TPA response element, a response element for phorbol esters. **2** **thyroid response element**. *See* **response element**.

trefoil motif *an alternative name for* **P domain**.

trehalose α-D-glucopyranosyl-α-D-glucopyranoside; α,α-trehalose; a nonreducing disaccharide, *also known as* **mushroom sugar** *or* **mycose**, that acts as a reserve carbohydrate in certain fungi (especially yeasts), algae, and lichens. It is cleaved by trehalase but not by most other α-glucosidases. It

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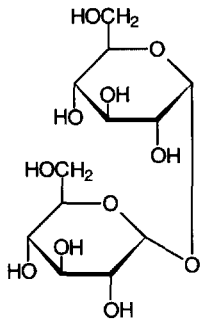
is a component of **cord factors**, which are a mixture of trehalose 6,6′-mycolates (*see* **mycolic acid**). α-D-Glucopyranosyl-β-D-glucopyranoside (α,β-trehalose) and β-D-glucopyranosyl-β-D-glucopyranoside (β,β-trehalose) occur naturally, but only very rarely.



tremerogen any of a group of oligopeptides that contain non-amino-acid components and are the sex hormones of the jelly fungi. They induce formation of a conjugation tube in compatible cell types. They may contain a farnesyl group bound to cysteine.

Tresyl *proprietary name* indicating the 2,2,2-trifluoroethane sulfonyl group; Tresyl-activated Sepharose can be used in the preparation of affinity gels, the sulfonyl groups being readily displaceable by amines, thiols, phenolic groups, or imidazole, which remain bound to the gel as the stationary component; e.g.

$$\text{support–O–SO}_2\text{–CH}_2\text{–CF}_3 + \text{RSH} = \text{support–S–R} + \text{HOSO}_2\text{–CH}_2\text{–CF}_3.$$

tretinoin *a WHO-approved nonproprietary name for* **retinoic acid**, especially for pharmacological use.

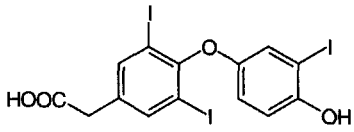
TRF *abbr. for* **1** thyrotropin-releasing factor; i.e. **thyrotropin-releasing hormone**. **2** T-cell-replacing factor; *see* **interleukin 5**.

TRF-III *or* **TRF-m** *see* **interleukin 1**.

TRH *abbr. for* thyrotropin-releasing hormone.

tri+ *comb. form* **1** denoting three, threefold, thrice, every third; *see also* **tris+ 2** *(in chemical nomenclature)* (*distinguish from* **tris+** (def. 2)) **a** indicating the presence in a molecular entity of three identical specified unsubstituted groups, e.g. trichloroethylene, trimethylamine. **b** indicating the presence in a molecular entity of three identical oxoacid residues in linear anhydride linkage; e.g. adenosine 5′-triphosphate.

triac *(informal) abbr. for* 3,3′,5-triiodothyroacetic acid, a catabolite of **thyroxine**.



triaconta+ *or (before a vowel)* **triacont+** *comb. form* denoting thirty or thirty times.

triacontanoic acid melissic acid; a 30-carbon straight-chain aliphatic acid; m.p. 93.6 °C (methyl ester 71.5 °C).

triacontapeptide a 30-residue peptide.

triacylglycerol *or (formerly)* **triglyceride** any triester of glycerol; the three fatty acids may all be the same, or differ in any permutation. Triacylglycerols are important components of plant oils, animal fats, and animal plasma lipoproteins. The degree of unsaturation of the component fatty acids determines the melting point: plant oils, which typically contain a high percentage of (poly)unsaturated fatty acids, are liquid, while animal fats, being more highly saturated, are solid or semisolid. *See also* **lipoprotein** and individual plant oils and animal fats.

triacylglycerol lipase EC 3.1.1.3; *systematic name*: triacylglycerol acylhydrolase; *other names*: lipase; triglyceride lipase; tributyrase. An enzyme that catalyses the reaction:

$$\text{triacylglycerol} + H_2O = \text{diacylglycerol} + \text{fatty-acid anion}.$$

This is a very widespread enzyme activity, with types ranging from those found in microorganisms to those such as **pancreatic lipase**, and the hormone-sensitive lipase of mammalian adipose tissue. Example from *Pseudomonas aeruginosa* (precursor): database code LIP_PSEAE, 311 amino acids (32.69 kDa). Example from *Geotrichum candidum* (yeast): database code NRL_1THG, 544 amino acids (59.62 kDa); 3-D structure known; the latter is a globulin with mainly alpha helix and turns, and contains one modified glutamine residue (pyrrolidone carboxylic acid).

triadin a major membrane glycoprotein of the sarcoplasmic reticulum triad junction of skeletal and cardiac muscle. The luminal domain has a highly conserved region and can bind both the ryanodine receptor and calsequestrin. Example from rabbit: database code A45990, 706 amino acids (79.04 kDa).

+triaose *suffix* used in nomenclature of glycolipids to indicate a molecule containing an oligosaccharide moiety composed of three sugar residues (which may be the same or different), as in gangliotriaose. *Distinguish from* **triose**.

triazine-dye affinity chromatography *(sometimes)* a type of **dye-ligand chromatography** in which the coupled dye is a triazinyl compound. The technique is not **affinity chromatography** in the original sense.

tricaprin *a trivial name for* **tridecanoin**, the triacylglycerol containing three caproyl (decanoyl) residues. *See also* **tricaproin**, **tricaprylin**.

tricaproin *a trivial name for* **trihexanoin**, the triacylglycerol containing three capric (hexanoic) ester residues. *See also* **tricaprin**, **tricaprylin**.

tricaprylin *a trival name for* **trioctanoin**, the triacylglycerol containing three caprylic (octanoic) ester residues. *See also* **tricaprin**, **tricaproin**.

tricarboxylic acid *abbr.*: TCA; any organic compound having three carboxylic-acid groups. The name often has the connotation of relationship with **citric acid**, as in the **tricarboxylic-acid cycle**.

tricarboxylic-acid cycle (*abbr.*: TCA cycle) *or* **citric-acid cycle** *or* **Krebs cycle** a nearly universal metabolic pathway in which the acetyl group of acetyl coenzyme A is effectively oxidized to two CO_2 and four pairs of electrons are transferred to coenzymes. The acetyl group combines with oxaloacetate to form citrate, which undergoes successive transformations to isocitrate, 2-oxoglutarate, succinyl-CoA, succinate, fumarate, malate, and oxaloacetate again, thus completing the cycle. In eukaryotes the tricarboxylic acid is confined to the mitochondria. *See also* **glyoxylate cycle**.

trichloroacetic acid *abbr.*: TCA; Cl_3CCOOH; an organic acid widely used for the precipitation of protein from tissue and other cell extracts. A final concentration of 3–9% (w/w) is normally used. TCA can be extracted into diethyl ether.

trichloroethyl alcohol 2,2,2-trichloroethanol; an active metabolite of chloral hydrate with CNS depressant actions.

trichohyalin a structural protein produced and retained in cells of the inner root sheath and medulla of the hair follicle. In the sheep, 75% of its amino acids are glutamate or glutamine, arginine, or lysine; the gene is also expressed in epithelia, hoof, and rumen. Trichohyalin associates in regular arrays with keratin intermediate filaments. Example from human: database code TRHY_HUMAN, 1898 amino acids (246.95 kDa).

tricine *or* **TRICINE** *trivial name for N*-tris[(hydroxy-

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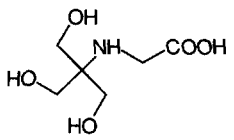
methyl)methyl]glycine; *N*-[2-hydroxy-1,1-bis(hydroxymethyl)-ethyl]glycine; a **Good buffer substance**; p*K* (20 °C) = 8.15.



tricosa+ *or (before a vowel)* **tricos+** *comb. form* denoting twenty-three or twenty-three times.

tricosapeptide a 23-residue peptide.

trideca+ *or (before a vowel)* **tridec+** denoting thirteen or thirteen times.

tridentate **1** having three teeth or toothlike projections. **2** (of a **ligand**) chelating a metal ion by means of three donor atoms.

triene any alkatriene or substituted alkatriene.

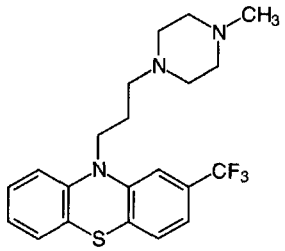
+triene(+) *or (before a vowel)* **+triene** *(in chemical nomenclature) infix or suffix* in systematic names denoting the presence in a molecular structure of an unsaturated aliphatic hydrocarbon chain containing three (conjugated or unconjugated) double bonds. The position of each double bond may be indicated by a locant for its lowest numbered carbon atom; e.g. cycloheptatriene, icosa-8,11,14-trienoic acid.

trienoic indicating a compound having a carboxylic-acid group and an aliphatic chain with three double bonds.

trienoyl indicating the acyl group of a trienoic acid.

triflavin a **disintegrin** from the snake *Trimeresurus flavoviridis*, containing an Arg-Gly-Asp (**RGD**) motif at residues 49–51, that inhibits fibrinogen interaction with platelet receptors, and thereby inhibits platelet aggregation. Database code DIST_TRIFL, 70 amino acids (7.57 kDa).

trifluoperazine 10-[3-(4-methyl-1-piperazinyl)propyl]-2-(trifluoromethyl)-10*H*-phenothiazine; an antagonist with high affinity for D_2 **dopamine receptors**. It is used in the treatment of manic and schizophrenic psychoses and as an inhibitor of **calmodulin** action. *One proprietary name*: Stelazine (dihydrochloride).



trifluoroacetic acid *abbr.*: THA; CF_3COOH; a strong organic acid. It is widely used as a catalyst in organic synthesis, and is used to cleave Cbz– and tBoc– groups from protected amino acids. The anhydride is used to prepare trifluoroacetyl derivatives for the protection of alcohols and amines, and as volatile derivatives for gas–liquid chromatography.

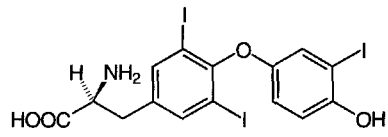
trigger **1** to induce (often rapidly) into activity. **2** a mechanism or agent that brings about such an action. The term is commonly used in connection with membrane receptor activation and signal transduction, as in trigger mechanism.

triglyceride *a former name for* **triacylglycerol**; the term is still quite commonly used as in, e.g., 'triglyceride fraction', but use is discouraged for such purposes since triglyceride is properly a generic term for compounds having three glyceryl residues (e.g. **cardiolipin**).

trigonelline nicotinic acid *N*-methylbetaine; 3-carboxy-1-methylpyridium inner salt; a metabolite of nicotinic acid. It is excreted in the urine after the consumption of relatively large amounts of nicotinic acid.

trihydric (of a chemical compound) containing three hydroxyl groups per molecule; trihydroxy; used especially of alcohols.

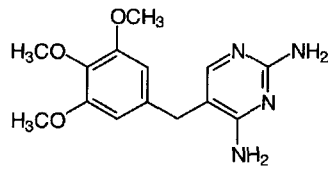
triiodothyronine *abbr.*: T_3; 3,3,5-triiodo-L-thyronine; one of the hormones secreted by the thyroid gland. Plasma levels of T_3 are much lower than those of **thyroxine** (T_4) (20- to 50-fold), but the physiological activity of T_3 is higher. The mechanism of action of thyroid hormones involves T_3 binding to a **thyroid-hormone receptor**, which is then activated to bind to **thyroid response element**, a transcription-regulatory element. Much of T_4 is converted to T_3 within cells, T_3 being the compound that binds to the thyroid-hormone receptor in target cells. *See also* **thyroglobulin**.



trilaurin a triacylglycerol in which all the fatty-acyl moieties are **lauroyl** (dodecanoyl).

trimer a molecular complex having three components or subunits. If these are identical, it is referred to as a **homotrimer**; if any one is different from any other, it is called a **heterotrimer**. —**trimeric** *adj.*

trimethoprim 2,4-diamino-5-(3,4,5-trimethoxybenzyl)pyrimidine; a specific inhibitor of formylation and a competitive inhibitor of **dihydrofolate reductase**. The trimethoprim resistance gene can be used as a selectable marker for cloning vectors in animals or plants. *See also* **sulfamethoxazole**.



trimethylaminuria *see* **fish-odour syndrome**.

trimyristin a triacylglycerol in which all the fatty-acyl moieties are **myristoyl** (tetradecanoyl).

trinactin a neutral macrotetralide antibiotic with an action similar to that of **nonactin**.

trinitroglycerin glyceryl trinitrate; trinitroglycerol; the nitrate moiety is metabolized to nitrite and, subsequently, to **nitric oxide** and nitrosothiol, which activate guanylate cyclase. The resulting increase in cyclic GMP synthesis may explain the potent vasodilator effects of this and similar organic nitrates.

trinor+ *prefix (in a trivial name of a compound)* indicating replacement of three methyl groups by hydrogen. *See also* **nor+**.

trinucleotide repeat an increase in copy number of a normally polymorphic triplet. Some genetic disorders, e.g. **fragile X syndrome**, result from this.

triol any aliphatic chain having three hydroxyl groups.

triolein a triacylglycerol in which all the fatty-acyl moieties are **oleoyl** (*cis*-9-octadecenoyl). *See also* **triolein breath-test**.

triolein breath-test a test used as an alternative to fecal fat determination to test for intestinal malabsorption of fat. When ^{14}C-labelled triacylglycerol (10 μCi) is administered by mouth, a proportion of the ^{14}C will be breathed out as $^{14}CO_2$, which is trapped in a solution of hyamine carbonate for scintillation counting.

triose **1** any one of three monosaccharides having a chain of three carbon atoms in the molecule, these being the chiral enantiomers D- and L-**glyceraldehyde**, and their achiral constitutional isomer **glycerone**. **2** trisaccharide; used as a stem name for any oligosaccharide consisting of three residues per mol-

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ecule of the same sugar in a single type of linkage, as in maltotriose. *Distinguish from* **+triaose**.

triose phosphate *general term for* D-glyceraldehyde 3-phosphate, glycerone phosphate, or a mixture thereof. These two compounds are interconvertible by the enzyme **triose-phosphate isomerase**.

triosephosphate dehydrogenase (NADP$^+$) *see* **glyceraldehyde-3-phosphate dehydrogenase (NADP$^+$) (phosphorylating)**.

triose-phosphate isomerase EC 5.3.1.1; *systematic name*: D-glyceraldehyde-3-phosphate ketol-isomerase; *other names*: triosephosphate mutase; phosphotriose isomerase. The sugar **isomerase** enzyme that is important in the glycolytic pathway, and catalyses the aldose–ketose isomerization of the two **triose phosphates**, i.e. the reaction:

D-glyceraldehyde 3-phosphate = glycerone phosphate.

Example from *Saccharomyces cerevisiae*: database code NRL_1YPIA, 247 amino acids (26.63 kDa); 3-D structure known.

trioxsalen 2,5,9-trimethyl-7*H*-furo[3,2-*g*][*1*]-benzopyran-7-one; 4,5′,8-trimethylpsoralen (*abbr.*: TMP); a pigmentation agent (photosensitizer). *See also* **psoralen**.

tripalmitin a triacylglycerol in which all the fatty-acyl moieties are **palmitoyl** (hexadecanoyl).

tripeptide a three-residue peptide.

triphenylmethyl group *abbr.*: trityl; a group used in chemical syntheses to protect nitrogen, sulfur, and, particularly, oxygen functions as their trityl derivatives. It has the advantage that, while stable under many conditions, it is readily removed by mild acid. It can be introduced by reagents such as triphenylmethyl chloride.

triphosphate **1** the pentavalent ion, $P_3O_{10}^{5-}$, derived from triphosphoric acid, decaoxotriphosphoric(V) acid, $(HO)_2PO–O–PO(OH)–O–PO(OH)_2$ (an acid not known in the free state). **2** any mixture of the anions of triphosphoric acid. **3** any (partial or full) salt or ester of triphosphoric acid. **4** any organic compound containing three phosphoric residues linked linearly by oxygen atoms. **5** name of the univalent group $–O–PO(OH)–O–PO(OH)–O–PO(OH)_2$ (irrespective of its state of ionization). **6** *(formerly)* any organic compound containing three independent phosphoric residues attached to different parts of the molecule; now incorrect, use **trisphosphate**.

triphospho+ **1** *prefix* to a chemical name indicating the presence in ester linkage of a triphosphoric residue. **2** *(formerly) prefix* to a chemical name indicating the presence of three independent phosphoric residues in ester linkages; now incorrect, use **trisphospho+**.

triphosphoinositide *abbr.*: TPI; *a former name for* **phosphatidylinositol 4,5-bisphosphate** (*symbol*: PtdIns-4,5-P_2). Current nomenclature requires bisphosphate, trisphosphate, etc. for the substituent phosphates on the inositol moiety. Other phosphatidylinositol bisphosphates are known, e.g. PtdIns-phosphatidylinositol 3,4-biphosphate.

triphosphopyridine nucleotide (oxidized) *abbr.*: TPN$^+$; *an obsolete name for* **nicotinamide-adenine dinucleotide phosphate**.

triphosphopyridine nucleotide (reduced) *abbr.*: TPNH; *an obsolete name for* **nicotinamide-adenine dinucleotide phosphate (reduced)**.

triphosphoric *symbol*: *PPP or* (in the one-letter convention for nucleotides) ppp; *general name for* a residue of triphosphoric acid, $(HO)_2PO–O–PO(OH)–O-PO(OH)_2$, whether singly or multiply attached through oxygen to other groups and whether or not any residual hydroxyl groups are dissociated.

triple bolus test *see* **combined test of pituitary function**.

triple helix **1** the superhelically coiled arrangement of the three polypeptide chains in **tropocollagen**. **2** *or (sometimes)* **triplex** *see* **triplex DNA**.

triple membrane *see* **unit membrane**.

triple point the point on a phase diagram at which three phases may coexist.

triplet **1** *(in molecular biology)* any sequence of three purine and/or pyrimidine bases in nucleic acids that specifies a particular amino acid. It is synonymous with **codon** in mRNA or **anticodon** in DNA or tRNA. *See also* **synonym triplet**. **2** a collection of three of a kind. **3** any one of three offspring born from a single pregnancy.

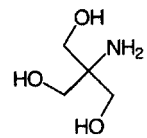
triplet code the **genetic code**, which is based on **triplets** (def. 1) of purine and pyrimidine bases.

triplex DNA a three-stranded structure formed by duplex DNA in association with an oligonucleotide, when purine or pyrimidine bases occupy the major groove of the DNA double helix adopting **Hoogsteen base pairing** with the Watson–Crick base pairs. Triplex DNA may be involved as an intermediate in **crossing over**. *See also* **tetraplex DNA**.

triploid **1** describing a cell, tissue, or organism having three times the haploid (monoploid) number of chromosomes. **2** such a cell, tissue, or organism. —**triploidy** *n.*

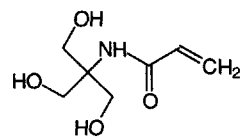
tris+ *prefix* **1** denoting three times, thrice, tripled; *see also* **tri+** (def. 1). **2** *(in chemical nomenclature)* (*distinguish from* **tri+** (def. 2)) **a** indicating the presence in a molecular entity of three identical specified groups each substituted in the same way; e.g. tris(2-hydroxyethyl)amine. **b** indicating the presence at separate positions in a molecular entity of three identical inorganic oxoacid residues; e.g. inositol 1,4,5-trisphosphate.

Tris *or* **TRIS** *or* **THAM** tris(hydroxymethyl)aminomethane; 2-amino-2-hydroxymethyl-1,3-propanediol; a compound widely used as a biological buffer substance in the pH range 7–9; pK_a (20 °C) = 8.3; pK_a (37 °C) = 7.82.



trisaccharide an **oligosaccharide** with three **monosaccharide** units.

Trisacryl **1** *a proprietary name for* *N*-acryloyl-2-amino-2-hydroxymethyl-1,3-propanediol; $CH_2=CH–CO–NH–C(CH_2OH)_3$; a compound used in the manufacture, by copolymerization with a cross-linking agent such as *N,N′*-diallyl L-tartardiamide (*abbr.*: DATD) or *N,N′*-methylenebisacrylamide, of a range of strongly hydrophilic artificial support materials of controlled porosity that are useful for gel-permeation chromatography. Copolymerization with a cationic or anionic derivative as a third component yields support materials of utility in ion-exchange chromatography. Such materials are thermally, chemically, and biologically stable, and resistant to high pressures. **2** *as modifier* describing a range, or any member of a range, of such chromatographic support materials; e.g. Trisacryl polymers, Trisacryl ion-exchangers, Trisacryl gels, Trisacryl GF05, DEAE–Trisacryl M.



triskelion a hexamer of **clathrin** molecules, composed of three heavy chains and three light chains. In the **electron microscope** triskelions appear to have three bent arms each linked into a central point. [From triskele, a symbolic figure consisting of three legs radiating from a common centre.]

trisomic **1** describing a cell, tissue, or organism having three copies of one or more chromosome(s) in an otherwise diploid chromosome set. In humans, trisomy 21 (i.e. presence of three

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copies of chromosome 21) is asssociated with **Down's syndrome**. **2** such a cell, tissue, or organism. —**trisomy** *n.*

trisphosphate any compound containing three independent phosphoric residues in ester linkages, at positions indicated by locants; e.g. inositol 1,4,5-trisphosphate. *Compare* **triphosphate**.

trisphospho+ *prefix* to a chemical name indicating the presence of three independent phosphoric residues in ester linkages, at positions indicated by locants. *Compare* **triphospho+**.

tristearin a triacylglycerol in which all the fatty-acyl moieties are **stearoyl** (octadecanoyl).

tritiate to combine or label with **tritium**; to replace one or more atoms of hydrogen with tritium. Tritium may be introduced into specific sites by chemical synthesis but ^{3}H-labelled steroids are prepared by the reduction of unsaturated precursors with $^3H_2$, the number of ^{3}H atoms introduced depending upon the degree of unsaturation of the precursor and the catalyst used. Biosynthesis is rarely used for ^{3}H-labelling since intramolecular migration of ^{3}H atoms is often caused by enzymes.

tritin a type I **ribosome-inactivating protein** from wheat.

tritium the radioactive isotope of hydrogen, $^3_1$H (i.e. the nucleus contains two neutrons and one proton). It decays to produce β particles of low energy (0.018 MeV); half-life 12.26 years. *Compare* **deuterium**, **protium**.

tritium nuclear magnetic resonance spectroscopy *abbr.*: tritium NMR spectroscopy *or* TNMR spectroscopy; the application of **nuclear magnetic resonance spectroscopy** to determine the positions and extents of tritium substitution in substances (generally of known structure) that have been labelled with tritium (^{3}H). The technique depends upon an equality of the displacements of the resonance frequencies (chemical shifts) of tritium and protium (^{1}H) nuclei in corresponding environments relative to those occurring with the tritiated and nontritiated forms, respectively, of a reference substance. The method is quick, nondestructive, and applicable to very small amounts of material. It is thus particularly useful for determining the pattern of labelling in substances that are costly, complex in structure, and/or unstable. The technique is also used to follow the chemical and steric course of biochemical reaction sequences.

triton **1** *(in chemistry) symbol*: $^3H^+$; the cation derived from an atom of **tritium**; a **hydron** of nucleon number 3. **2** *(in nuclear physics) symbol*: t; a particle having a charge equal and opposite to that of an electron and having a mass of 3.0155 Da.

Triton *the proprietary name for* any of a series of polyoxyethylene ethers of certain alkylphenols that are surfactants and classed as nonionic detergents. Those used most commonly are based on the formula *tert*-octyl-C_6H_4–$[OCH_2CH_2]_x$OH; e.g. in Triton X-45, $x \approx 5$; in Triton X-100, $x = 9$ or 10 (aggregation number 100–155, CMC 0.2–0.9 mM); in Triton X-405, $x \approx 40$; Triton CF is a benzyl-polyoxyethylene *tert*-octylphenyl ether; Triton N-101 is a polyoxyethylene nonylphenyl ether (C_9H_{19}–C_6H_4–$[OCH_2CH_2]_x$OH), with $x = 9$ or 10.

tritosome a **lysosome** that is loaded with Triton. Tritosomes have an isopycnic density in sucrose solution of about 1.14, and can thus be separated readily from other cell constituents.

tritriaconta+ *or (before a vowel)* **tritriacont+** *comb. form* denoting thirty-three or thirty-three times.

triturate **1** to rub or grind (solid material) to a very fine powder either dry or in a liquid. **2** a finely ground powder or an even mixture of finely ground powders, especially powdered drugs.

trituration **1** the act of triturating or the condition of being triturated; *see* **triturate** (def. 1). **2** the composing of a dental amalgam.

trityl *trivial name for* the **triphenylmethyl group**.

trivial name *(in chemical nomenclature)* a name of a chemical species that has no part of it used in a systematic sense; e.g. xanthophyll, urea. It generally has historical or colloquial origins, and refers to attributes such as appearance or source. It makes no pretension to describe molecular structure. The adjective 'trivial' has no perjorative meaning, numerous compounds of biochemical interest having approved or recommended trivial names. *Compare* **descriptive name**, **systematic name**.

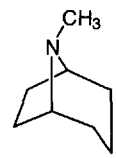
trixenic *see* **synxenic**.

trk a protooncogene encoding a transmembrane glycoprotein selectively expressed in the developing nervous system; the product is a tyrosine kinase receptor, the expression of which is restricted *in vivo* to certain neurons of neural crest origin, or, as its counterpart *trkB*, in cells of the neuroepithelium. It is required for high-affinity binding of nerve growth factor, and neurotrophins 3 and 4 and is essential for signal transduction in their action. Example of receptor from human (precursor): database code TRKA_HUMAN, 790 amino acids (86.88 kDa). It was discovered as the transforming factor of a colon carcinoma and was originally known as *onc*D. The oncogenic activity resulted from a genomic rearrangement event in which nonmuscle tropomyosin sequences were aberrantly fused onto the transmembrane and cytoplasmic domains of Trk (tropomyosin receptor kinase).

tRNA *abbr. for* transfer RNA.

Trojan horse inhibitor *see* **affinity label**.

tropane 8-methyl-8-azabicyclo[3.2.1]octane; the basic ring system in tropane alkaloids.



+trope *suffix* denoting turning.

+troph *suffix* denoting an organism with a specified mode of nutrition, e.g. **autotroph**, **chemotroph**.

trophic of, or concerning, nourishment, nutrition. *Compare* **tropic** (def. 1).

+trophic *suffix* denoting nourishment, nutrition; e.g. organotrophic, saprotrophic. *See also* **+tropic**.

+trophin *noun suffix* denoting a substance having a **trophic** function. *See also* **+tropin**.

tropho+ *or (before a vowel)* **troph+** *comb. form* denoting food or nourishment.

trophoblast the outer part of the blastocyst stage of a mammalian conceptus. Its outermost layer consists of syncytial cells concerned with penetration and implantation into the uterine endometrium; these cells secrete extracellular hydrolases that facilitate movement of the blastocyst into the previously organized endometrial structure.

+trophy *noun suffix* **1** denoting food or nourishment. **2** denoting growth or size.

tropic **1** *or (sometimes, esp. Brit.)* **trophic** having a stimulating effect (especially of a hormone, etc.). **2** of or relating to a **tropism**.

+tropic *or (sometimes, esp. Brit.)* **+trophic** *suffix* denoting a stimulatory function; e.g. gonadotropic. *See also* **+trophic**, **+tropin**.

tropic acid α-phenyl-β-hydroxypropionic acid; (*S*)3-hydroxy-2-phenylpropanoic acid; a compound that occurs in ester form in **atropine** and other tropane alkaloids.

+tropin *or (sometimes, esp. Brit.)* **+trophin** *noun suffix* denoting a substance having a stimulatory function, especially a hormone produced by the adenohypophysis. *See also* **+trophin**.

tropine tropan-3α-ol; 2-hydroxytropane; *N*-methyl-8-azabicyclo[3.2.1]octan-3-ol; **atropine** is the ester with (±)-tropic acid. Tropine is a *meso* structure. The –OH group is *trans* to the CH_3N– group. In the geometrical isomer, **pseudotropine**, this relationship is *cis*.

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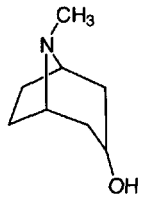
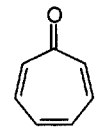


tropine



tropone

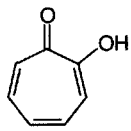
tropinone *N*-methyl-8-azabicyclo[3.2.1]octan-3-one; the oxidation product of **tropine**.

tropism movement directed towards some positive stimulus, or away from some negative stimulus.

+tropism *noun suffix* denoting a specific type of **tropism** as indicated by the prefixed word.

tropocollagen *or* **soluble collagen** a rod-shaped molecule, 3000 Å long and 15 Å in diameter, consisting of two α1 and one α2 polypeptide chains each of about 1000 amino-acid residues, of which about a third are glycine and 21% are proline plus hydroxyproline. They also contain hydroxylysine. The three polypeptide chains wind around each other to form a superhelical cable; the chains are hydrogen-bonded to each other. Tropocollagen fibres spontaneously associate with each other, with their N-terminal sequences overlapping C-terminal sequences of adjacent chains in a staggered array, to form **collagen** molecules. *Compare* **procollagen**. *See also* **registration peptide**.

tropolone 2-hydroxy-2,4,6-cycloheptatrien-1-one; a structure found in some mould metabolites and in **colchicine**.



tropomodulin a cytoskeletal tropomyosin-regulatory protein that binds to the end of erythrocyte tropomyosin and blocks its head-to-tail association along actin filaments; it does not bind to F actin. It has no homology to other proteins. Its modulation of the spectrin–actin complex in the erythrocyte membrane skeleton affects the viscoelastic properties of erythrocytes. Example from human: database code TMOD_HUMAN, 359 amino acids (40.52 kDa).

tropomyosin a protein found in smooth, skeletal, and cardiac muscle. It comprises α and β subunits and is bound to **actin** forming a component of the **troponin** complex that regulates calcium-dependent binding of actin and myosin and, consequently, muscle contraction. Tropomyosin forms a characteristic coiled coil with a prominent seven-residue periodicity (five motifs). Different isoforms are produced by differential splicing; e.g. isoforms of α-tropomyosin differ in striated and smooth muscle. Example from human fibroblasts: database code TPM3_HUMAN, 284 amino acids (32.84 kDa).

tropomyosin kinase EC 2.7.1.132; an enzyme that catalyses the phosphorylation by ATP of tropomyosin to form *O*-phosphotropomyosin with release of ADP.

tropone 2,4,6-cycloheptatrien-1-one.

troponin *abbr.*: Tn; a central regulatory protein of striated muscle contraction, comprising three subunits: **troponin T** (Tn-T), which binds to **tropomyosin**; **troponin I** (Tn-I), which regulates actinomyosin ATPase; and **troponin C** (Tn-C), which binds Ca^{2+} and with Ca^{2+} bound abolishes the inhibition on the binding of myosin to actin filaments produced by the other two troponins. Examples, Tn-T (human slow skeletal muscle isoform): database code TRT1_HUMAN, 277 amino acids (32.77 kDa). Tn-I (human cardiac muscle form): database code TRIC_HUMAN, 209 amino acids (23.85 kDa). Tn-C (human slow skeletal and cardiac form; bovine and porcine sequences are the same): database code TPCC_HUMAN, 161 amino acids (18.40 kDa).

+tropy *noun suffix* denoting turning.

Trp *symbol for* a residue of the α-amino acid L-tryptophan (alternative to W).

Trp-2 tyrosinase-related protein 2; this is a product of the *tyrp-2* gene. *See also* ***slaty***.

***trp* genes** a family of tryptophan biosynthetic genes found in bacteria. The following examples of *trp* gene products are all from *Escherichia coli*.

(1) TrpA (database code TRPA_ ECOLI, 268 amino acids (28.69 kDa)) and TrpB (database code TRPB_ECOLI, 396 amino acids (42.80 kDa)) are the α and β subunits of tryptophan synthase (EC 4.2.1.20); it catalyses the formation of L-tryptophan from L-serine and 1-(indol-3-yl) glycerol 3-phosphate; glyceraldehyde 3-phosphate is also formed. The enzyme is a tetramer (α_2,β_2); the subunits have half-activities (α for aldol cleavage of indoleglycerol phosphate and β for tryptophan synthesis).

(2) TrpC (database code TRPC_ECOLI, 452 amino acids (49.36 kDa)) is a monomeric bifunctional enzyme: the 'TrpF domain' is ***N*-(5′-phosphoribosyl)anthranilate isomerase** (EC 5.3.1.24); it catalyses the interconversion of *N*-5′-phosphoribosyl-anthranilate and 1-(2-carboxyphenylamino)-1-deoxy-D-ribulose 5-phosphate. The 'TrpC domain' is **indole-3-glycerol-phosphate synthase** (EC 4.1.1.48; *abbr.*: IGPS); it catalyses the decarboxylation of 1-(2-carboxyphenylamino)-1-deoxy-D-ribulose 5-phosphate to form 1-(indol-3-yl) glycerol 3-phosphate, CO_2, and H_2O.

(3) TrpE/G, **anthranilate synthase** (EC 4.1.3.27); it catalyses a reaction between chorismate and L-glutamine to form anthranilate, pyruvate, and L-glutamate. This enzyme is a tetramer with two molecules of component I – TrpE, database code TRPE_ECOLI, 520 amino acids (57.46 kDa) – and two of component II – TrpG, TRPG_ECOLI, 530 amino acids (56.68 kDa). (4) TrpR, aporepressor (*trp* is co-repressor) for the operators of the *trp* operon, *trpR* itself, and *aroH*; a homodimer of known 3-D structure; database code TRPR_ECOLI, 107 amino acids (12.21 kDa).

true cholinesterase *an alternative name for* **acetylcholinesterase**.

truncate **1** to shorten by cutting. **2** to terminate prematurely. —**truncation** *n.*

Trypan Blue a blue dye that is water-soluble and possesses sulfate and amino groups, whose charge prevents it from penetrating the plasma membrane of healthy cells. Dead cells or cells with damaged membranes take it up, making it a useful

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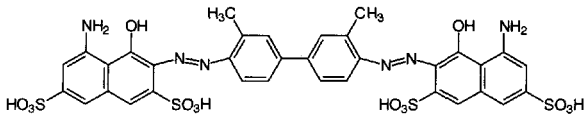
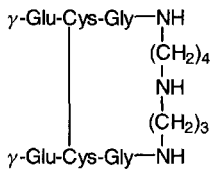
stain for determining cell viability (*see* **dye-exclusion test**). It does, however, stain healthy macrophages.



trypanosomatid *a common word for* any protozoan of the order **Kinetoplastida**, which includes **trypanosomes** and other genera.

trypanosome any member of the genus *Trypanosoma* (order **Kinetoplastida**), comprising parasitic flagellate protozoans. Infection causes disease (trypanosomiasis) in a range of animals. In humans there are two main forms of the disease: African trypanosomiasis (or sleeping sickness), which is caused by *T. brucei* and transmitted by tsetse flies, and South American trypanosomiasis (or Chagas' disease), which is caused by *T. cruzi* and transmitted by insects such as the assassin bug. Invasion of the nervous system, with attendant signs, is more common with the African form than with the South American form, which mainly affects the heart.

trypanothione the oxidized form of N^1,N^6-bis(glutathionyl)spermidine; a compound purified from the trypanosomatid *Crithidia fasciculata*, a parasite of insects. Members of the **Kinetoplastida** lack **glutathione reductase**, and **glutathione** is converted to the conjugate, trypanothione. *See also* **trypanothione reductase**.



trypanothione reductase EC 1.6.4.8; *systematic name*: NADPH:trypanothione oxidoreductase; an enzyme found uniquely in **trypanosomatids**, and hence a potential chemotherapeutic target. It catalyses the reaction:

NADPH + trypanothione =
NADP$^+$ + reduced trypanothione;

FAD is a cofactor. Example from *Trypanosoma cruzi* (homodimer): database code TYTR_TRCR, 492 amino acids (53.81 kDa). *See also* **trypanothione**.

trypsin EC 3.4.21.4; a serine endopeptidase occurring in two forms, known as α and β trypsin. These result from proteolytic cleavage, β being formed directly from the precursor, **trypsinogen**, and α and other forms by further cleavage. Trypsin is of major importance in protein digestion in the small intestine, trypsinogen being a constituent of **pancreatic juice**. Trypsin is also widely used as a proteolytic agent experimentally, e.g. in protein sequencing. It preferentially cleaves at Arg-|-Xaa and Lys-|-Xaa. Example (bovine): database code NRL_1NTP, 223 amino acids (23.28 kDa); 3-D structure known. *See also* **trypsin inhibitor**.

trypsin inhibitor any of various naturally occurring substances that inhibit the activity of **trypsin**. The most-studied example is bovine pancreatic trypsin inhibitor (*see* **pancreatic trypsin inhibitor**). *See also* **soybean trypsin inhibitor**.

trypsinize *or* **trypsinise** to treat something, especially intact cells or membrane preparations with trypsin. Cells are released from adhesion to tissue-culture plates by trypsinization; treatment of membranes with trypsin can be used to indicate exposure of protein domains, as subsequent analysis will reveal unattacked bonds that might be expected to be broken, indicating that they may be shielded from attack by inclusion within the membrane. — **trypsinization** *or* **trypsinisation** *n*.

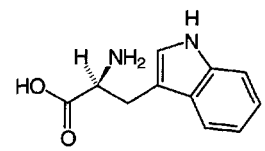
trypsinogen the pancreatic **zymogen** precursor of **trypsin**. It is secreted in **pancreatic juice** and in the duodenum is cleaved by **enteropeptidase**, which cleaves the Lys^{23}-|-Ile^{24} (in the precursor; in the mature molecule, these are Lys^8-|-Ile^9) bond in trypsinogen, to yield β trypsin. Example, human precursor TRY1_HUMAN, 247 amino acids (26.56 kDa); residues 1–15 are the signal peptide, 16–247 trypsinogen (residues 16–23 are a propeptide).

tryptamine *β*-3-indolylethylamine; 3-(2-aminoethyl)indole; 2-(1*H*-indol-3-yl)ethanamine; $(C_8H_6N)CH_2–CH_2–NH_2$; a biogenic amine, formed by enzymic decarboxylation of tryptophan. Of widespread occurrence in mammalian tissues, it is found also in plants and is a product of microbial degradation of proteinaceous material.

tryptase EC 3.4.21.59; *other names*: mast cell tryptase; mast cell protease II; skin tryptase; lung tryptase; pituitary tryptase. An enzyme that catalyses the preferential cleavage: Arg-|-Xaa, Lys-|-Xaa, but with more restricted specificity than **trypsin**. It is a trypsin-like serine endopeptidase released from the secretory granules upon mast-cell activation. Example β-tryptase from human (precursor) homotetramer: database code TRYB_HUMAN, 275 amino acids (30.49 kDa). Cytotoxic T-lymphocyte tryptase, or CTL tryptase, is also known as **granzyme A**.

tryptic of, or relating to, trypsin; effected or produced by the action of trypsin; especially **tryptic digestion**, the partial hydrolysis of a protein by trypsin.

tryptophan *or (formerly)* **tryptophane** *the trivial name for β*-3-indolylalanine; *α*-amino-*β*-3-indolepropionic acid; 2-amino-3-(1*H*-indol-3-yl)propanoic acid; $(C_8H_6N)CH_2–CH(NH_2)–COOH$; a chiral *α*-amino acid. L-tryptophan (*symbol*: W *or* Trp), (*S*)-2-amino-3-(1*H*-indol-3-yl)propanoic acid, is a coded amino acid found in peptide linkage in proteins; codon: UGA (only in mitochondria) or UGG. In mammals it is an essential dietary amino acid and is glycogenic. The peptide antibiotic, **tyrocidin** C, contains one residue per molecule of D-tryptophan (*symbol*: D-Trp *or* DTrp), (*R*)-2-amino-3-(1*H*-indol-3-yl)propanoic acid.



L-tryptophan

tryptophanal *α*-amino-*β*-3-indolepropionaldehyde; 2-amino-3-(1*H*-indol-3-yl)propanal; $(C_8H_6N)CH_2–CH(NH_2)–CHO$; the *α*-amino-aldehyde analogue of **tryptophan**.

tryptophanase **1** EC 4.1.99.1; *recommended name*: tryptophanase; *systematic name*: L-tryptophan indole-lyase (deaminating). An enzyme that catalyses a reaction between water and L-tryptophan to form indole, pyruvate, and NH_3. It is responsible for indole formation in *Escherichia coli* and other enteric bacteria and bacilli. The reaction is comparable to that of β-tyrosinase (*see* **tyrosinase** (def. 2)). **2** *an alternative name for* **tryptophan 2,3-dioxygenase**.

tryptophanate **1** tryptophan anion; the anion, $(C_8H_6N)CH_2–CH(NH_2)–COO^–$, derived from **tryptophan**. **2** any salt in which tryptophan is anionic. **3** any ester of tryptophan.

tryptophan 2,3-dioxygenase EC 1.13.11.11; *systematic name*: L-tryptophan:oxygen 2,3-oxidoreductase (decyclizing); *other names*: tryptophan pyrrolase; tryptophanase; tryptophan oxygenase; tryptamine 2,3-dioxygenase. An enzyme that catalyses a reaction between dioxygen and L-tryptophan to form L-

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formylkynurenine. It is a heme protein in mammalian liver, and it shows broad specificity towards tryptamine and derivatives including D- and L-tryptophan, 5-hydroxytryptophan, and serotonin. Example (homotetramer) from rat: database code T230_RAT, 406 amino acids (47.80 kDa).

tryptophan 5-hydroxylase EC 1.14.16.4; *recommended name*: tryptophan 5-monooxygenase; *systematic name*: L-tryptophan,tetrahydrobiopterin:oxygen oxidoreductase (5-hydroxylating); *other name*: tryptophan oxygenase. An enzyme that catalyses a reaction between dioxygen, L-tryptophan, and tetrahydrobiopterin to form 5-hydroxy-L-tryptophan, dihydrobiopterin, and water. This is the rate-limiting enzyme in the biosynthesis of the neurotransmitter **5-hydroxytryptamine**. Example from rat: database code TR5H_RAT, 444 amino acids (51.01 kDa).

tryptophanium *tryptophan cation*; the cation, $(C_8H_6N)CH_2–CH(NH_3^+)–COOH$, derived from **tryptophan**.

tryptophan 2-monooxygenase EC 1.13.12.3; *systematic name*: L-tryptophan:oxygen 2-oxidoreductase (decarboxylating); *other name*: tryptophan oxygenase. An enzyme that catalyses a reaction between dioxygen and L-tryptophan to form indole-3-acetamide, CO_2, and water. This is the first step in **auxin** biosynthesis. Example from *Pseudomonas syringae*: database code TR2M_PSESS, 557 amino acids (61.79 kDa).

tryptophan 5-monooxygenase *the recommended name for* **tryptophan 5-hydroxylase**.

tryptophano the alkylamino group, $(C_8H_6N)CH_2–CH(COOH)–NH–$, derived from **tryptophan**.

tryptophanol 3-(2-amino-3-hydroxypropyl)indole; 2-amino-3-(1*H*-indol-3-yl)propanol; $(C_8H_6N)CH_2–CH(NH_2)–CH_2OH$; the α-amino-alcohol analogue of **tryptophan**.

tryptophan oxygenase *an alternative name for* **1 tryptophan 2,3-dioxygenase**. **2 tryptophan 2-monooxygenase**. **3 tryptophan 5-hydroxylase**.

tryptophan pyrrolase *an alternative name for* **tryptophan 2,3-dioxygenase**.

tryptophan repressor *see* ***trp*** **genes**.

tryptophan synthase *see* ***trp*** **genes**.

tryptophan tryptophylquinone *abbr.*: TTQ; a quinoprotein cofactor of methylamine dehydrogenase, EC 1.4.99.3, an enzyme of methylotropic bacteria. TTQ consists of a tryptophanyl side-chain cross-linked to the tryptophyl 6,7-dione side-chain of a modified tryptophan residue.

tryptophyl the acyl group, $(C_8H_6N)CH_2–CH(NH_2)–CO–$, derived from **tryptophan**.

TSF *abbr. for* thymocyte-stimulating factor, i.e. **interleukin 2**.

TSH *abbr. for* thyroid-stimulating hormone.

T state *see* **T form**.

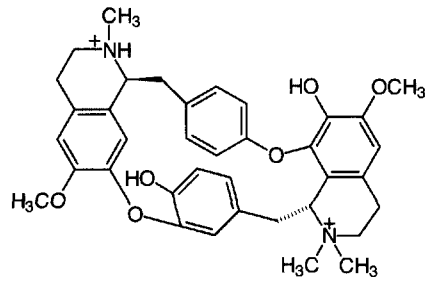
TTP *abbr. for* **1** ribosylthymine triphosphate *or* ribothymidine triphosphate, *common names for* ribosylthymine 5′-triphosphate, ribothymidine 5′-triphosphate, 5′ribothymidylyl triphosphate, thymine riboside 5′-triphosphate. **2** *(sometimes)* thymidine triphosphate. dTTP is recommended.

TTQ *abbr. for* tryptophan tryptophylquinone.

T tubule *abbr. for* transverse tubule; a type of tubule in a muscle fibre that arises as an invagination of the plasma membrane and penetrates the fibre, running mostly transversely among the fibrils and surrounding each of them with a ring. Each ring is shared by adjacent fibrils and the whole forms an intercommunicating system of tubules across the fibre. The function of these tubules is to pass the excitation signal from the muscle cell plasma membrane to the sarcomeres, ensuring rapid and synchronous activation. *See also* **sarcoplasmic reticulum**.

TTX *abbr. for* tetrodotoxin.

tubocurarine (+)-tubocurarine is the active principle of **curare**; it is a nicotinic cholinergic receptor competitive antagonist, and is used as a muscle relaxant. The molecule contains groups that are arranged in space in a rigid framework such that the atoms of acetylcholine that are important in its action have the correct geometry. In particular, two positively charged nitrogens are fixed at a distance of 1.4 nm, possibly corresponding to the N^+ atoms of two acetylcholine molecules. Tubocurarine competes with acetylcholine at the neuromuscular junction and the endplate potential falls dramatically. The spacing of N^+ atoms appears crucial to the action of drugs such as **suxamethonium**.



(+)-tubocurarine

tubulin a widely distributed globular subunit protein, profilaments of which form the structural elements of a **microtubule**. It is a heterodimer of two chains, α and β, each ≈50 kDa. The stable form of isolated tubulin is a dimer in which α–β pairing is believed to predominate; such a heterodimer is also the basic component of the microtubule. The dimer binds two molecules of GTP, one at an exchangeable site on the β chain and one at a nonexchangeable site on the α chain. The GTP is hydrolysed to GDP at the plus end, more slowly than assembly of heterodimers, to give a GTP cap at that end. GDP–tubulin is disassembled more readily than GTP–tubulin, so the rate of GTP hydrolysis could regulate tubulin assembly. Examples from human; α-1: database code TBA1_HUMAN, 451 amino acids (50.10 kDa); β-1: database code TBB1_HUMAN, 444 amino acids (49.70 kDa).

***α*-tubulin acetylase** *see* **tubulin *N*-acetyltransferase**.

tubulin *N*-acetyltransferase EC 2.3.1.108; *other name*: α-tubulin acetylase; an enzyme that catalyses the reaction:

acetyl-CoA + α-tubulin L-lysine =
CoA + α-tubulin N^6-acetyl-L-lysine.

tubulinyl-Tyr carboxypeptidase EC 3.4.17.17; *other names*: carboxypeptidase-tubulin; soluble carboxypeptidase; an enzyme that catalyses the cleavage of the Glu-|-Tyr bond to release the C-terminal tyrosine residue from the native tyrosinated tubulin. It is inactive on carbobenzoxy-Glu-Tyr.

tuftelin *or* **enamelin** an acidic enamel protein of teeth with a composition similar to tuft proteins. It is found in association with the crystal component and secreted at a very early stage of enamel formation in vertebrate teeth. Example (bovine): database code ENAM_BOVIN, 389 amino acids (43.81 kDa).

tuftsin the tetrapeptide Thr-Lys-Pro-Arg, isolable from **leukokinin** (leukophilic human IgG); the sequence occurs in the Fc fragment of IgG. The tetrapeptide binds to and stimulates the bactericidal, phagocytic, and tumoricidal activities of macrophages and granulocytes, and may also stimulate the migration of polymorphonuclear leukocytes. [After Tufts University, where it was discovered.]

tumble **1** to rotate in a plane vertical to the axis of rotation; 'head over heels'. Proteins and other macromolecules tumble in solution whereas integral membrane proteins rotate on an axis normal to the plane of the membrane but cannot tumble through the membrane surface. **2** in bacterial chemotaxis, to change direction by a rapid reversal of the direction of flagellar rotation, the bacterium then 'tumbling' in response to Brownian motion.

tumor *a variant spelling (esp. US) of* **tumour**.

tumorigenic describing a substance or treatment that has the

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tendency to cause the formation of a **tumour**.

tumour *or (esp. US)* **tumor** a mass of proliferating cells lacking, to varying degrees, normal growth control. Tumours may be benign, i.e. proliferating very slowly, or malignant, i.e. growing aggressively, invading neighbouring tissues, and spreading to distant parts of the body by releasing cells into the bloodstream or lymph. These cells form secondary tumours (*see* **metastasis**). *See also* **adenoma**, **carcinoma**, **lymphoma**, **sarcoma**. —**tumorous** *or* **tumoral** *adj.*

tumour initiator any compound having the ability, when administered to an animal, to cause the formation of a tumour.

tumour necrosis factor *abbr.*: TNF; either of two structurally and functionally related proteins: TNF-α is produced mainly by monocytes and macrophages, whereas TNF-β is produced by lymphoid cells. The two proteins are about 30% homologous at the amino-acid level, and bind to the same cell-surface receptors; both exist as homotrimers. Both TNF-α (cachectin) and TNF-β (lymphotoxin) were originally thought of as selective antitumour agents, but are now known to have a multiplicity of actions. In binding to their receptors, present on virtually all cells examined, they activate a large array of cellular genes and also multiple signal-transduction pathways, kinases, and transcription factors. Their genes are single-copy genes, closely linked within the MHC cluster. *See* **tumour necrosis factor α**; **tumour necrosis factor β**, **tumour necrosis factor receptor**.

tumour necrosis factor α (*abbr.*: TNF-α) *or (formerly)* **cachectin** a **cytokine** that is produced by macrophages, monocytes, endothelial cells, neutrophils, smooth muscle cells, activated lymphocytes, and astrocytes. It is a transmembrane glycoprotein and cytotoxin with a variety of functions, including the ability to mediate the expression of genes for growth factors, cytokines, transcription factors, and receptors. It can cause cytolysis of certain tumour cell lines, it has been implicated in the induction of cachexia (but *see* **cachectic factor**), it is a potent pyrogen, causing fever by direct action or by stimulation of interleukin 1 secretion, and it can stimulate cell proliferation and induce cell differentiation under certain conditions. The molecule is a homotrimer. Example: database code NRL_1TNFA, 152 amino acids (16.82 kDa); 3-D structure known (high beta content, disulfide bond). *See also* **tumour necrosis factor**.

tumour necrosis factor β (*abbr.*: TNF-β) *or (formerly)* **lymphotoxin** a **cytokine** produced by T lymphocytes that is cytotoxic for a wide range of tumour cells. It binds to the same ligands as **tumour necrosis factor α**. Example from human (precursor): database code TNFB_HUMAN, 205 amino acids (22.27 kDa). *See also* **tumour necrosis factor**.

tumour necrosis factor receptor *abbr.*: TNF receptor; either of two distinct receptors for **tumour necrosis factor** (TNF), one of M_r 55 000 and the other of 75 000. The two types have related extracellular domains, based on cDNA sequencing, and these are also related to the extracellular domains of nerve growth factor receptor and some other cell-surface molecules. These form a receptor family characterized by four domains with regularly spaced cysteine residues; each has a single transmembrane domain; the intracellular domains show no significant homologies. Either TNF receptor type alone appears sufficient for high-affinity binding and full biological activity, and binds either **tumour necrosis factor α** or **tumour necrosis factor β** with high affinity. The signal transduction mechanism remains speculative, but receptor activation leads to a number of events, including activation of protein kinase C, protein kinase A, phospholipase A_2, and phosphatidylcholine-specific phospholipase C, and accumulation of cyclic AMP and diacylglycerol. Example, tumour necrosis factor receptor 1 precursor from *Rattus norvegicus*: database code TNR1_RAT, 461 amino acids (50.97 kDa).

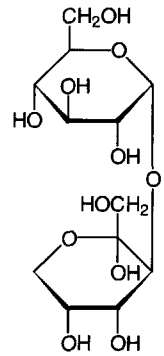
tumour promoter any compound that, when administered to an animal, sensitizes tissues to the action of a **tumour initiator**, or predisposes tissue to become tumorous in any other way, such that tumours form in greater numbers or grow more rapidly than if a tumour promoter had not been administered.

tumour-suppressor gene a normal gene one function of which is to suppress tumorigenesis. Certain cancers have been shown to be associated with mutant tumour-suppressor genes; *see* (e.g.) **p53**, ***RB***.

tunnel effect the phenomenon in which an electron or a proton, because of its small mass, does not behave kinetically according to the laws of classical mechanics. These particles can sometimes penetrate an energy barrier that is greater than their kinetic energy.

turacin *see* **tetrapyrrole**.

turanose 3-*O*-α-D-glucopyranosyl-D-fructose; an early product of the acid hydrolysis of **melezitose**.



turbid (of a solution) opaque due to the presence of suspended particles. —**turbidity** *n.*

turbidimeter an instrument for measuring the degree to which turbidity hinders the passage of light through a solution.

turbidimetry the quantitative determination of the concentration of substances in suspension by measurement of the decrease in light transmission caused by the suspended particles. *Compare* **nephelometry**.

turnaround sequence (in DNA) a sequence of nucleotides between two **inverted repeats**. A turnaround sequence will cause a 'bubble' of noncomplementary nucleotides at one end of a **hairpin**.

turnover number an obsolete expression of enzymic activity, variously defined on different occasions as the number of substrate molecules converted to product per catalytic site per minute, or as the number of moles of substrate converted per mole of enzyme per minute or second; it has the dimension of reciprocal time. *Compare* **catalytic constant**, **katal**.

turret a multiple cuvette holder that rotates in a spectrophotometer.

Tween *the proprietary name for* a series of surfactants based on polyoxyethylene sorbitan esters. For example, Tween 20 is polyoxyethylene sorbitanmonolaurate (CMC 0.059 mM). Similarly the sorbitan moiety in other Tweens is: Tween 40, sorbitanmonopalmitate; Tween 60, sorbitanmonostearate; Tween 65, sorbitantristearate; Tween 80, sorbitanmonooleate (aggregation number 58, CMC 0.012 mM); Tween 85, sorbitantrioleate.

twist a *Drosophila* gene for a ***MYC*** family **helix-turn-helix** transcription factor involved in the establishment of germ layers. It is a homodimer. Database code TWST_DROME, 490 amino acids (54.34 kDa).

twist conformation **1** a median conformation of a nonplanar, six-membered, saturated ring compound through which one **boat conformation** passes during conversion into another boat conformation, or through which a boat conformation passes during conversion into a **chair conformation** or vice versa. It is similar to **skew conformation** (def. 1). **2** any conformation of the five-membered ring form of a monosaccha-

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ride or monosaccharide derivative when three adjacent ring atoms are coplanar and the other two lie on opposite sides of the plane. The conformational descriptor *-T* may be added to the name of such a compound. *See also* **conformation**.

twist number *or* **twisting number** *symbol*: T; the total number of base pairs in a DNA molecule divided by the number of bases per turn of the double helix. It is one of the properties that identifies **topological isomers** of DNA. *See also* **linking number**, **writhing number**.

twitchin the protein product of *unc-22*, one of about 40 genes important for muscle assembly and function in the nematode *Caenorhabditis elegans*. Twitchin is a giant myosin-associated protein (*compare* **titin**) that is autophosphorylated on threonine; repeats are homologous to **fibronectin** type III. The protein was named for a mutation that results in twitching. Database code S07571, 6048 amino acids (667.72 kDa). It has a counterpart in *Aplysia californica* and presumably other invertebrates.

two-carbon fragment **1** any group of atoms containing two carbon atoms. **2** *an early term for* a metabolically active acetyl radical, as in acetyl coenzyme A.

two-dimensional chromatography a chromatographic method in which separation is first effected in one direction and, after rotation of the chromatogram through 90°, then in a second direction, often with a different solvent (or a different pH). **Two-dimensional electrophoresis** works on the same principle.

two-dimensional polymer a macromolecular structure in which approximately parallel chains extending in one direction are cross-linked by another series of approximately parallel chains extending in a second direction. Bacterial cell-wall peptidoglycans are two-dimensional polymers with glycan chains extending in one direction that are cross-linked to peptide chains.

TXA *abbr. for* thromboxane A (*see* **thromboxane**).

TXB *abbr. for* thromboxane B (*see* **thromboxane**).

Tylenol *see* **acetaminophen**.

tyndallization *or* **tyndallisation** a method of sterilization in which the sample is heated at 80–100 °C on successive days, with a period of incubation in between. The aim is to kill cells on each occasion, but to allow spores (which are not killed by heating) to germinate to produce susceptible cells during the periods of incubation. [After John Tyndall (1820–93), British natural philosopher, alpinist, and popularizer of science.]

type III system a protein secretory system found in Gram-negative bacteria that is responsible for the secretion of proteins known as **Yop**. The system is known as type III because it was the third type of secretory system found in the membrane of Gram-negative bacteria.

typing *(in immunology)* the identification of the classes of histocompatibility antigens, blood groups, or other surface markers present in a sample of serum, or on white blood cells or red blood cells.

Tyr *symbol for* a residue of the α-amino acid L-tyrosine (alternative to Y).

tyramine tyrosamine; *p*-(β-aminoethyl)phenol; 2-(4-hydroxyphenyl)ethylamine; a biogenic amine with adrenergic action, formed by enzymic decarboxylation of tyrosine. Of widespread occurrence in mammalian tissues, it is also found in several plant species and in **ergot**, and is a product of microbial action in the intestine, in the putrefaction of animal tissue, and in the ripening of cheese.

Tyr(I_2) *or* (if the context does not imply the locants) **Tyr(3,5-I_2)** *symbol for* a residue of the α-amino acid 3,5-diiodo-L-tyrosine (*see* **diiodotyrosine**).

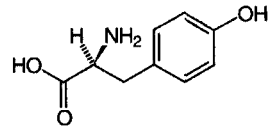
tyrocidine *or* **tyrocidin** any of several peptide antibiotics produced by *Bacillus brevis* that are cyclic decapeptides. The structure of tyrocidine A is (amino acids are L unless otherwise stated) cyclic -Leu-D-Phe-Pro-Phe-D-Phe-Asn-Gln-Tyr-Val-Orn-. Tyrocidine B is similar, but with L-Tyr in place of L-Phe, and in tyrocidine C D-Trp replaces the D-Phe attached to the Asn. Structurally tyrocidines are similar to **gramicidin S**, and they have a similar action, increasing the permeability of bacterial membranes, promoting leakage of cytoplasmic constituents, and permitting entry into the cell of ions larger than those normally transported. *Bacillus brevis* is immune from this action. This group of compounds has little application in medicine. Biosynthesis is independent of ribosomes (*see* **protein and peptide biosynthesis**).

Tyrode's solution *or* **Tyrode solution** *or* **Ringer–Tyrode solution** a balanced salt solution modified from **Locke's solution**, initially for experiments on mammalian intestine. The solution usually contains (in g L^{-1}, approx.): NaCl (8.0); KCl (0.2); $MgCl_2{\cdot}6H_2O$ (0.1); $CaCl_2$ (anhydrous, 0.2); $NaHCO_3$ (0.1); $NaH_2PO_4{\cdot}H_2O$ (0.05); and glucose (1.0). [After Maurice Vejux Tyrode (1878–1930), US pharmacologist, who devised this solution in 1910.]

tyrosinase **1** *an alternative name for* **monophenol monooxygenase**. **2** **β-tyrosinase** EC 4.1.99.2; *recommended name*: tyrosine phenol-lyase; an enzyme that catalyses a reaction between L-tyrosine and water to form phenol, pyruvate, and NH_3. Pyridoxal-phosphate is a coenzyme. The protein is a homotetramer, similar to **tryptophanase** (def. 1). Example from *Citrobacter freundii*: database code TPL_CITFR, 456 amino acids (51.44 kDa).

tyrosinate **1** tyrosinate(1–); tyrosine monoanion. In theory, the term denotes any ion or mixture of ions formed from **tyrosine** and having a net charge of –1, although the species $HO{-}C_6H_4{-}CH_2{-}CH(NH_2){-}COO^-$ predominates in practice. **2** *the systematic name for* tyrosinate(2–); tyrosine dianion; $^-O{-}C_6H_4{-}CH_2{-}CH(NH_2){-}COO^-$. **3** any salt containing an anion of tyrosine. **4** any ester of tyrosine.

tyrosine *the trivial name for* β-(*p*-hydroxyphenyl)alanine; α-amino-*p*-hydroxyhydrocinnamic acid; α-amino-β-(*p*-hydroxyphenyl)propionic acid; 3-(4-hydroxyphenyl)alanine; 2-amino-3-(4-hydroxyphenyl)propanoic acid; $HO{-}C_6H_4{-}CH_2{-}CH(NH_2){-}COOH$; a chiral α-amino acid. L-Tyrosine (*symbol*: Y *or* Tyr), (*S*)-2-amino-3-(4-hydroxyphenyl)propanoic acid, is a coded amino acid found in peptide linkage in proteins; codon: UAC or UAU. In mammals it is an essential dietary amino acid, and is both glucogenic and ketogenic. One residue per molecule of D-tyrosine (*symbol*: D-Tyr *or* DTyr), (*R*)-2-amino-3-(4-hydroxyphenyl)propanoic acid, occurs as its *O*-methyl ether in the antibiotic cycloheptamycin.



L-tyrosine

tyrosine decarboxylase EC 4.1.1.25; an enzyme that catalyses the decarboxylation of L-tyrosine to **tyramine**. Pyridoxal-phosphate is a coenzyme. Example from parsley: database code A44405, 514 amino acids (57.38 kDa).

tyrosine hydroxylase EC 1.14.16.2; *recommended name*: tyrosine 3-monooxygenase; *systematic name*: L-tyrosine, tetrahydrobiopterin:oxygen oxidoreductase. An enzyme that catalyses a reaction between dioxygen, L-tyrosine, and tetrahydrobiopterin to form 3,4-dihydroxy-L-phenylalanine, dihydrobiopterin, and water; it requires ferric ion. It is the rate-limiting enzyme in the synthesis of **catecholamine** neurotransmitters. In humans four types are produced by alternative splicing. Example, type 3: database code TY3H_HUMAN, 528 amino acids (58.46 kDa).

tyrosine kinase EC 2.7.1.112; *recommended name*: protein-tyrosine kinase; *other names*: tyrosylprotein kinase; protein kinase (tyrosine); hydroxyaryl-protein kinase. An enzyme that

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transfers the terminal phosphate of ATP to a specific tyrosine residue on its target protein; i.e. it catalyses the phosphorylation by ATP of protein-tyrosine to form protein-tyrosine phosphate with release of ADP. The enzyme molecule has five motifs. The tyrosine kinase family is of profound importance due to its involvement in the signalling processes associated with mitogenic stimulation, cell growth, and oncogenesis. The tyrosine kinases fall into two major classes, those that are cell membrane receptors and integral membrane proteins, and those that are intracellular and function downstream of the receptors. The membrane receptors have been grouped into subclasses according to their structure (all individual polypeptides have a single transmembrane domain, with the kinase activity in an intracellular domain); examples include subclass I, proteins having two cysteine-rich repeat sequences in the extracellular domain of a monomeric receptor, a group that includes the **epidermal growth factor receptor**; subclass II, disulfide-linked heterotetrameric $\alpha_2\beta_2$ structures with extracellular cysteine-rich repeat sequences similar to subclass I, an example being the **insulin receptor**; subclass III, proteins with five immunoglobulin-like repeats in the extracellular domain, and with a non-kinase insert in the kinase region, typified by the **platelet-derived growth factor receptor**; and subclass IV, proteins with three immunoglobulin-like repeats in the extracellular domain, with a non-kinase insert in the kinase region. This classification continues to be extended. The intracellular non-receptor tyrosine kinases include, among many, the products of ***FGR***, ***FYN***, and ***src***. *See also* **protein kinase**.

tyrosine 3-monooxygenase *the recommended name for* **tyrosine hydroxylase**.

tyrosine transaminase *or* **tyrosine aminotransferase** (*abbr.*: TAT) EC 2.6.1.5; *systematic name*: L-tyrosine:2-oxoglutarate aminotransferase; an enzyme that catalyses the reaction:

L-tyrosine + 2-oxoglutarate =
4-hydroxyphenylpyruvate + L-glutamate.

It is a pyridoxal-phosphate enzyme and it catalyses the first step in tyrosine catabolism; defects lead to tyrosinemia type II (**Richner–Ranhart syndrome**). Example from human (homodimer): database code ATTY_HUMAN, 454 amino acids (50.34 kDa).

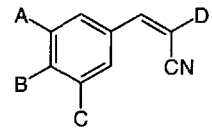
tyrosinium tyrosine cation; the cation, $HO–C_6H_4–CH_2–CH(NH_3^+)–COOH$, derived from **tyrosine**.

tyrosino the alkylamino group, $HO–C_6H_4–CH_2–CH(COOH)–NH–$, derived from **tyrosine**.

tyrosin-*O*^{4}-yl the aryloxy group, $HOOC–CH(NH_2)–CH_2–C_6H_4–O–$, derived from **tyrosine**.

tyrosyl the acyl group, $HO–C_6H_4–CH_2–CH(NH_2)–CO–$, derived from **tyrosine**.

tyrphostin any of a series of inhibitors of protein tyrosine kinases. The structures are derived from the substituted benzylidenemalononitrile shown as the core structure; A, B, and C can be $–NO_2$, $(CH_3)_3C–$, –OH, or –H. In tyrphostin 25, [(3,4,5-trihydroxyphenyl)-methylene]-propanedinitrile, D is –CN. Other actions are known for some members of the series, including uncoupling of oxidative phosphorylation and inhibition of lipoxygenases.



tyrphostin 25

tyvelose *a trivial name for* the aldohexose 3,6-dideoxy-D-mannose, 3,6-dideoxy-D-*arabino*-hexose, a monosaccharide isolated from various lipopolysaccharides elaborated by some Gram-negative bacteria, e.g. certain serotypes of *Salmonella typhi*. In such serotypes it contributes to the antigenic specificity of the organism's O antigens. The L-enantiomer is separately named as **ascarylose**.

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Uu

u **1** *symbol for* unified atomic mass unit. **2** *see* **IU**.

u *symbol for* **1** speed (alternative to *v*, *w*, or *c*). **2** (bold italic) velocity (alternative to *v*, *w*, or *c*).

U *symbol for* **1** a residue of the base uracil in a nucleic-acid sequence. **2** a residue of the ribonucleoside uridine (alternative to Urd). **3** uniformly labelled. **4** enzyme unit (obsolete; superseded by **katal**). **5** uranium.

U *symbol for* **1** electric potential difference (alternative to ΔV or $\Delta\phi$). **2** internal energy.

U46619 a stable thromboxane A_2 analogue and mimetic; *another name for* **9,11-dideoxy-11α,9α-epoxymethanoprostaglandin $F_{2\alpha}$**.

UAA a codon in mRNA for chain termination; the **ochre codon**.

UAC a codon in mRNA for L-tyrosine.

UAG a codon in mRNA for chain termination; the **amber codon**.

UAS *abbr. for* upsteam activator sequence; the counterpart in yeast of an **enhancer**.

UAU a codon in mRNA for L-tyrosine.

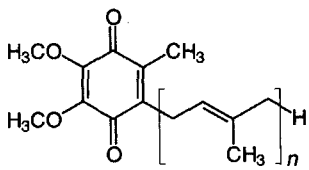
Ubbelohde viscometer *see* **capillary viscometer**.

UBIP *abbr. for* ubiquitous immunopoietic polypeptide.

ubiquinol *abbr.*: QH_2; reduced **ubiquinone**.

ubiquinol–cytochrome *c* reductase EC 1.10.2.2; *systematic name*: ubiquinol:ferricytochrome-*c* oxidoreductase; *other name*: complex III. An enzyme complex that catalyses the oxidation of ubiquinol by two molecules of ferricytochrome *c* to form ubiquinone and two molecules of ferrocytochrome *c*. It contains cytochromes b_{562}, b_{566}, and c_1, as well as nonheme iron and Fe–S complexes.

ubiquinone *or (formerly, but not recommended)* **coenzyme Q** *abbr.*: Q; a lipid-soluble electron-transporting coenzyme that is an essential component in the **respiratory chain**. The structure is shown in the diagram; *n* has values from 6 to about 12. The side-chain length is indicated by the abbreviation Q_n. Ubiquinone is biosynthesized in mammals from tyrosine, and in bacteria and other organisms by the **shikimate pathway**. *See also* **protonmotive Q cycle**.



ubiquinone reductase *see* **NADH dehydrogenase (ubiquinone)**.

ubiquitin **1** a small, highly conserved, heat-stable protein of 76 amino-acid residues first isolated from bovine thymus but subsequently found in the cells of all tissues studied, in animals, yeast, bacteria, and higher plants. Located in both nuclei and cytoplasm, it derives its name from its widespread distribution. It undergoes an ATP-dependent reaction with proteins that results in condensation of its terminus with lysine amino groups; this process is mediated by a large multiprotein complex, the 26S **proteasome**. For example, cyclin degradation in the control of the cell cycle is triggered by ubiquitination. Thus the cell has two means of protein degradation, ubiquitination and proteolysis in lysosomes. Such modified proteins are degraded rapidly. Ubiquitin is synthesized as a polyubiquitin precursor with exact head-to-tail repeats, the number of repeats differing between species. In some species there is a final amino acid after the last repeat (e.g. Val in human). Some ubiquitin genes encode a single copy of ubiquitin fused to a ribosomal protein. Human, bovine, and porcine ubiquitins and those from long-tailed hamster, rat, mouse, rabbit, *Xenopus laevis*, and the following insects – *Drosophila melanogaster*, *Ceratitis capitata*, *Spodoptera frugiperda*, and *Manduca sexta* – all have the sequence: MQIFVKTLTGKTITLEVEPSDTIENVKAKIQDKEGIPPDQQRLIFAGKQLEDGRTLSDYNIQKESTLHLVLRLRGG. Example from human: database code UBIQ_HUMAN, 76 amino acids (8.56 kDa); 3-D structure known; database code; NRL_1UBQ; three motifs. **2** *a former name for* **ubiquitous immunopoietic polypeptide**.

ubiquitin activating enzyme E1 an enzyme that activates ubiquitin by first adenylylating, with ATP as co-substrate, its C-terminal glycine residue and thereafter linking this to itself via the side chain of a cysteine residue, releasing AMP. The protein is a monomer and can accommodate two ubiquitin molecules. Example from human: database code UBA1_HUMAN, 1058 amino acids (117.66 kDa).

ubiquitin-conjugating enzyme *see* **ubiquitin–protein ligase**.

ubiquitin–protein ligase EC 6.3.2.19; *other names*: ubiquitin-conjugating enzyme; ubiquitin-activating enzyme; an enzyme that couples ubiquitin to a protein lysine to form protein N-ubiquityllysine with hydrolysis of ATP to ADP and pyrophosphate. Examples from yeast: database code UBC1_YEAST, 215 amino acids (24.15 kDa); database code UBC2_YEAST, 172 amino acids (19.68 kDa); UBC3_YEAST, 295 amino acids (34.03 kDa); UBC8_YEAST, 218 amino acids (24.61 kDa). Examples from human: database code UBC2_HUMAN (also in rat and rabbit), 152 amino acids (17.29 kDa); UBC8_HUMAN, 183 amino acids (20.63 kDa).

ubiquitous immunopoietic polypeptide *abbr.*: UBIP; a polypeptide that has lymphocyte-differentiating properties and can stimulate adenylate cyclase. It is involved in maintenance of chromatin structure, regulation of gene expression, stress response, and ribosome biogenesis. It was formerly called ubiquitin. *See also* **proteasome**.

UCA a codon in mRNA for L-serine.

UCC a codon in mRNA for L-serine.

UCG a codon in mRNA for L-serine.

UCP *abbr. for* brown fat uncoupling protein.

UCU a codon in mRNA for L-serine.

Udo *symbol for* the undecanoyl group, CH_3–$[CH_2]_9$–CO–.

UDP *abbr. for* uridine (5′-)diphosphate.

UDP-*N*-acetylglucosamine 6-dehydrogenase EC 1.1.1.136; an enzyme that catalyses the reaction:

UDP-*N*-acetyl-D-glucosamine + 2 NAD^+ + H_2O = UDP-*N*-acetyl-2-amino-2-deoxy-D-glucuronate + 2 NADH.

UDP-*N*-acetylglucosamine–dolichyl-phosphate-*N*-acetylglucosamine phosphotransferase EC 2.7.8.15; an enzyme that catalyses a reaction between UDP-*N*-acetyl-D-glucosamine and dolichyl phosphate to form *N*-acetyl-D-glucosaminyl-diphosphodolichol and UMP.

It catalyses the first reaction in the synthesis of oligosaccharide lipids. Example from Chinese hamster: database code UAGT_CRIGR, 408 amino acids (46.19 kDa).

UDP-*N*-acetylglucosamine 2-epimerase EC 5.1.3.14; an enzyme that catalyses the reaction:

UDP-*N*-acetyl-D-glucosamine = UDP-*N*-acetyl-D-mannosamine.

UDP-*N*-acetylglucosamine 4-epimerase EC 5.1.3.7; an enzyme that catalyses the reaction:

UDP-*N*-acetyl-D-glucosamine = UDP-*N*-acetyl-D-galactosamine.

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UDPG *abbr. for* uridinediphosphoglucose; UDPGlc is preferred (to avoid possible ambiguity in context with galactose).

UDPGal *or* **UDPgalactose** *abbr. for* uridinediphosphogalactose.

UDPgalactose 4-epimerase *an alternative name for* **UDPglucose 4-epimerase**.

UDPGlc *(preferred) abbr. for* uridinediphosphoglucose; *see also* **UDPG**.

UDPglucose 6-dehydrogenase EC 1.1.1.22; an enzyme that catalyses the reaction:

$$\text{UDPglucose} + 2\ \text{NAD}^+ + \text{H}_2\text{O} = \text{UDPglucuronate} + 2\ \text{NADH}.$$

Example from *Streptococcus pyogenes*: database code UDHG_STRPY, 402 amino acids (45.43 kDa).

UDPglucose 4-epimerase *the recommended name and systematic name for* the isomerase EC 5.1.3.2; *other names*: UDPgalactose 4-epimerase; *(formerly)* galactowaldenase; one of the enzymes that can interconvert uridinediphosphoglucose and uridinephosphogalactose. The mechanism involves oxidation of the C-4 hydroxyl group of the hexose moiety of either uridinediphosphosugar to an oxo group by a tightly bound molecule of NAD^+; the resultant NADH is then reoxidized by the intermediate oxo derivative with inversion of configuration of the resulting hydrogen and hydroxyl groups at C-4. *Compare* **UDPglucose–hexose-1-phosphate uridylyltransferase**. Example from *Escherichia coli*: database code GALE_ECOLI, 338 amino acids (37.22 kDa); 3-D structure known.

UDPglucose–hexose-1-phosphate uridylyltransferase EC 2.7.7.12; *systematic name*: UDPglucose:α-D-galactose-1-phosphate uridylyltransferase; *other names*: **uridyl transferase**; galactose-1-phosphate uridylyltransferase; one of the enzymes that can interconvert uridinediphosphoglucose and uridinediphosphogalactose. An enzyme important in the metabolism of galactose, it catalyses the exchange reaction:

$$\text{UDPglucose} + \alpha\text{-D-galactose 1-phosphate} = \alpha\text{-D-glucose 1-phosphate} + \text{UDPgalactose}.$$

A deficiency of the enzyme is associated with one form of **galactosemia**. Example from human: HUMGALT, 380 amino acids (43.01 kDa). *Compare* **UDPglucose 4-epimerase**.

UDPglucose pyrophosphorylase *an alternative name for* **UTP–glucose-1-phosphate uridylyltransferase**.

UDPglucuronate 4-epimerase EC 5.1.3.6; an enzyme that catalyses the reaction:

$$\text{UDP-D-glucuronate} = \text{UDP-D-galacturonate}.$$

UDPglucuronate 5′-epimerase EC 5.1.3.12; an enzyme that catalyses the reaction:

$$\text{UDP-D-glucuronate} = \text{UDP-L-iduronate}.$$

NAD^+ is a cofactor.

UDPglucuronosyltransferase EC 2.4.1.17; *abbr.*: UDPGT *or* UGT; *recommended name*: glucuronosyltransferase; an enzyme involved in the formation of **glucuronosides**. It catalyses a reaction between UDPglucuronate and an acceptor to form UDP and acceptor β-D-glucuronoside. There are many variants. The numbering follows several systems; the one followed here has UDPGT followed by a number, letter, and sometimes a number, e.g. UDPGT1F, UDPGT2B10. Examples from human: isozyme 1a precursor, microsomal (UDPGT1a) (bilirubin-specific isozyme 1): database code UD1A_HUMAN, 533 amino acids (59.52 kDa); UDGPT1b: database code UD1B_HUMAN, 530 amino acids (59.95 kDa); UDGPT1c (*other name*: UGT13): database code UD1C_HUMAN, 534 amino acids.

UDPGP *abbr. for* UDPglucose pyrophosphorylase (i.e. **UTP–glucose-1-phosphate uridylyltransferase**.

UGA **1** a codon in nonmitochondrial mRNA for chain termination; the **opal codon**. **2** a codon in mitochondrial mRNA for L-tryptophan.

UGC a codon in mRNA for L-cysteine.

UGG a codon in mitochondrial mRNA, and the only codon in nonmitochondrial mRNA, for L-tryptophan.

UGU a codon in mRNA for L-cysteine.

+ulose *noun suffix* denoting a **ketose**; it may be expanded to **+ulofuranose** or **+ulopyranose** according to whether the cyclic form of the sugar is five-membered or six-membered respectively.

+ulosonic acid *noun suffix* denoting a **ketoaldonic acid**; it may be expanded to **+ulofuranosonic acid** or **+ulopyranosonic acid** according to whether the cyclic form of the sugar acid is five-membered or six-membered respectively.

ultimate carcinogen *or* **ultimate carcinogenic metabolite** any metabolite of a **chemical carcinogen** that reacts with cellular constituents in a specific way to initiate carcinogenesis. *See also* **proximate carcinogen**.

ultimobranchial body one of a pair of glandlike structures derived during embryogenesis from the last branchial (gill) pouches. They occur in all vertebrates except cyclostomes. In most mammals they become embedded in the respective lobes of the thyroid gland, forming **C cells**, which secrete the polypeptide hormone **calcitonin**.

ultra+ *prefix* **1** beyond in space; on the other side (of). *Compare* **infra+**, **trans+**. **2** beyond a specified (esp. in scientific usage, lower) limit, range, value, etc. *Compare* **super+**. **3** beyond the common, ordinary, natural, etc.; extreme(ly). *Compare* **hyper+**.

ultracentrifuge any centrifuge that operates at high rotational velocities, i.e. one that generates high gravitational fields. Ultracentrifuges can be operated at known speeds with small variations and without temperature fluctuations. They may be either analytical or preparative.

ultradian (of a biological activity) occurring less often than once per 24-hour period. *Compare* **circadian**, **infradian**.

ultrafilter a filter of small pore size suitable for **ultrafiltration**.

ultrafiltration a separation process whereby a solution containing a solute of molecular size significantly greater than that of the solvent molecule is removed from the solvent by the application of a hydraulic pressure, which forces only the solvent to flow through a suitable membrane (usually one having a pore size in the range 0.001–0.1 μm), thereby concentrating the solute.

ultramicrotome a device for preparing very thin sections of cells or tissues, after fixing and embedding or freezing, for inspection in the transmission electron microscope.

ultrasonic of, pertaining to, or producing **ultrasound** waves.

ultrasonication the process of exposing material to **ultrasound**. It is used for cell disruption, for denaturation of proteins, and for cleaning solid surfaces. *See also* **sonicate**.

ultrasonic disintegrator an apparatus for disintegrating cells and other material, or for cleaning solid surfaces, by exposing them to **ultrasound**. *See also* **sonicator**.

ultrasound propagated waves, of the same nature as sound but inaudible, with frequencies of >20 kHz. Frequencies of ≈25 kHz can be used for disintegrating cells and subcellular components and also in cleaning baths for the removal of deposits on a wide variety of objects. In physiotherapy ultrasound in the range of 0.5–3 MHz is used for the relief of painful muscles and has its effect by the delivery of warmth and by changing the permeability of cell membranes which allows for the removal of fluid. For diagnostic purposes ultrasound in the range of 3–12 MHz is commonly used and is a popular method of non-invasive imaging e.g. in pregnant women. There is also ultrasonic microscopy which mimics light microscopy and employs sound in the GHz range. Ultrasound is also being developed for the disintegration of tumours using sound in the MHz range.

ultrastructure the fine structure of an organ, tissue, cell, or subcellular particle, especially that beyond the resolution of a light microscope but demonstrable with an electron microscope.

ultraviolet (radiation) *abbr.*: UV *or* uv; electromagnetic radiation of wavelengths in the range 13.6–400 nm (frequencies

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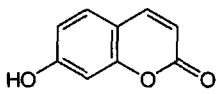
750 THz–22.1 PHz). This range overlaps the wavelengths of soft X-radiation and ends just across the short-wavelength limit of visible light. Ultraviolet radiation is often divided into **near ultraviolet** (200–400 nm) and **far ultraviolet** (or **vacuum ultraviolet**) (<200 nm); radiation in the far ultraviolet is absorbed by O_2 and requires the use of evacuated apparatus or flushing with N_2.

ultraviolet-endonuclease an enzyme involved in the repair of ultraviolet-irradiated DNA in microorganisms. *See also* **deoxyribonuclease (pyrimidine dimer)**, ***uvr***.

ultraviolet reactivation *see* **W reactivation**.

Ultrogel *the proprietary name for* a range of bead-form rigid support materials used in **gel filtration**, **affinity chromatography**, and related procedures. It consists of a lattice of polyacrylamide in a matrix of agarose gel.

umbelliferone 7-hydroxycoumarin; a common component of plant extracts, used as a fluorescent pH indicator and as a fluorescent label.



UMP *abbr. for* uridine monophosphate; i.e. uridine phosphate.

UMP synthase *a loose term applied to* the combination of enzymes that form uridine 5′-phosphate from orotate: these are ***orotate phosphoribosyltransferase*** (*forming orotidylic acid*) and **orotidine 5′-phosphate decarboxylase**. *See also* **uridine-5′-monophosphate synthase**.

umu bacterial genes encoding proteins that are involved in the error-prone **SOS repair** process, probably by allowing bypass synthesis across a damaged template. Protein examples from *Escherichia coli*: UmuC: database code UMUC_ECOLI, 422 amino acids (47.68 kDa); UmuD: database code UMUD_ECOLI, 139 amino acids (15.05 kDa).

un+ *prefix* **1** *(used with adjectives, adverbs, and nouns)* not; opposite of; contrary to. **2** *(used with verbs)* reversal of an action or state; release; removal from.

unary operator an arithmetic or logical operator (e.g. NOT) that operates on only one variable. *Compare* **binary operator**.

unc-86 a gene of *Caenorhabditis elegans* that encodes a transcription factor containing the **POU domain** and contributes to the naming of the domain. Example, Unc-86: database code UN86_CAEEL, 467 amino acids (52.31 kDa).

uncoating enzyme *(sometimes)* an enzyme that catalyses the removal of the protein coat from a virus.

uncoded amino acid *an alternative term for* **noncoded amino acid**.

uncompensated acidosis an **acidosis** in which there is a fall of the blood pH, due to the inadequacy of the physiological compensating mechanisms.

uncompensated alkalosis an **alkalosis** in which there is a rise of the blood pH, due to the inadequacy of the physiological compensating mechanisms.

uncompetitive inhibition the inhibition of the activity of an enzyme system when the inhibitor does not combine with the free enzyme, but only with one of the enzyme–substrate intermediates.

uncoupled **1** disconnected; unfastened. **2** *(in biochemistry)* describing an organism, tissue, cell, or mitochondrion in which phosphorylation is dissociated from oxidation in the **respiratory chain**. *See also* **uncoupling**.

uncoupler *an alternative name for* uncoupling agent (*see* **uncoupling**).

uncoupling *(in biochemistry)* the dissociation of phosphorylation from oxidation in the **respiratory chain**, so that electron transport proceeds without the esterification of phosphate and without the need for inorganic phosphate. An **uncoupling agent** (*or* uncoupler) is a substance that causes uncoupling of phosphorylation from electron transport at one or more points in the electron-transport chain. A classical example is **dinitrophenol**. Uncoupling agents probably act by causing leakage of protons across the mitochondrial inner membrane thereby destroying the proton gradient that drives oxidative phosphorylation. *See also* **chemiosmotic coupling hypothesis**.

uncoupling protein *see* **brown fat uncoupling protein**.

undec+ *or* **undeca+** *prefix* denoting eleven.

undecaprenol *or* **bactoprenol** a polyunsaturated long-chain (C_{55}) primary alcohol containing 11 **prenyl** units.

undecaprenyl phosphate *or* **undecaprenol phosphate** a very hydrophobic phosphate ester of **undecaprenol**. It acts as a membrane-soluble carrier to which intermediates are combined in the course of the biosynthesis of bacterial cell-envelope components, e.g. peptidoglycan and lipopolysaccharide. *Other names*: bactoprenyl phosphate; carrier lipid; C_{55} carrier lipid; C_{55} lipid carrier.

underivatized *or* **underivatised** (of a substance) in the naturally occurring state.

undulin a noncollagenous glycoprotein of the interstitial extracellular matrix, associated with collagen. Isolated from skin or placenta, it is found mainly between densely packed mature collagen fibrils as bundles of uniform wavy fibres. It is a member of the fibronectin–tenascin family, and is related to collagen type XIV. It is associated with dense collagen matrices in soft tissues and is likely to be involved in the supramolecular organization of interstitial collagens. Example (sequence fragments) from human, undulin 2: database code B40970, 445 amino acids (49.06 kDa); the sequence shows homology with fibronectin type III.

ung *see* **uracil-DNA *N*-glycosylase**.

Uni *see* **reactancy of enzymes**.

uni+ *comb. form* consisting of, having, or relating to one.

unified atomic mass unit *or (formerly)* **atomic mass unit** (*abbr.*: amu *or* a.m.u.) *symbol*: u; a non-SI unit of mass equal to one-twelfth of the mass of one atom of carbon-12; i.e.

$$1\ \mathrm{u} = m_a(^{12}\mathrm{C})/12 \approx 1.660\ 540 \times 10^{-27}\ \mathrm{kg}.$$

It is identical with **dalton**.

uniformly labelled *symbol*: U; describing a **labelled compound** in which the label is distributed in a statistically uniform, or nearly uniform, manner between all the possible positions in the molecule.

unimolecular reaction *see* **molecularity**.

uniparental disomy the inheritance of two copies of a chromosome from one parent.

uniport the process of noncoupled solute translocation or **facilitated diffusion**. The term includes reactions in which a single solute equilibrates across an osmotic barrier, normally mediated by a carrier protein known as a **uniporter**; e.g. the glucose-transport protein of mammalian erythrocytes. *Compare* **antiport**, **symport**.

unique (sequence) DNA *or* **single-copy DNA** any unique and specifically ordered nucleotide sequence in DNA that occurs only once in a genome. *Compare* **repetitive sequences**.

unit cell the smallest portion of a crystal that, by translation in three dimensions, is able to account for the structure of the entire crystal. The array of unit cells, arranged along parallel straight lines, makes up the **crystal lattice**.

unit membrane *or* **double membrane** *or* **triple membrane** any membrane, irrespective of cellular location, that on staining with osmium or other heavy metals appears in section in the electron microscope as a pair of parallel dark lines separated by a less dense layer, the whole being 6–10 nm thick. Unit membranes include the plasma membrane and the membranes of organelles such as mitochondria, nuclei, and endoplasmic reticulum.

unit of replication *see* **replicon**.

unit of transcription *see* **transcriptional unit**.

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univalent 1 *or* **monovalent** (of a chemical species) having a **valency** of one. 2 an unpaired chromosome seen during meiosis when bivalents are also present. Such a chromosome either lacks a homologue or results from **asynapsis**. —**univalency** *n.*

universal buffer mixture any solution containing several buffering systems chosen so as to provide a relatively high buffer capacity over a wide pH range.

universal donor an individual with O-type blood; such blood may be transfused into any recipient. *See* **ABO system**.

universal recipient an individual with AB-type blood; such individuals may be transfused with blood from any donor. *See* **ABO system**.

UNIX an **operating system** implemented on many current workstations and large computers.

unmediated transport *or* **nonmediated transport** the movement of a solute across a barrier by **diffusion** (def. 1).

unpaired electron an electron in an atom or molecule whose spin is not paired with the oppositely directed spin of another electron in the same atom or molecule. Only systems containing unpaired electrons will give an electron spin resonance signal. *See* **electron spin resonance spectroscopy**.

unsaponifiable lipid *or* **unsaponifiable material** part of a lipid sample that is not solubilized by **saponification**. It consists principally of steroids and terpenes.

unsaturated 1 (of a solution) able to dissolve more of the solute in question. 2 (of an organic compound) containing double bonds; *see also* **polyunsaturated**. 3 (of any chemical system, e.g. an enzyme or antibody) not fully saturated with ligand (e.g. substrate or antigen).

unsaturated-fatty-acid oxidation the degradation of unsaturated fatty acids to CO_2 and H_2O; this is achieved in large part by enzymes of the **beta-oxidation system**, but at certain points enzymes specific for unsaturated fatty acids are required. The first of these occurs when beta-oxidation reactions have removed carbons to the point at which the resulting acyl-CoA molecule has a Δ^3-*cis* double bond; this is not a substrate for **enoyl-CoA hydratase**, but an enoyl-CoA isomerase (*see* **dodecenoyl-CoA Δ-isomerase**) converts it to a substrate with a Δ^2-*trans* double bond. Another problem occurs when an acyl-CoA with a Δ^4-*cis* double bond is produced, which again is not a substrate for enoyl-CoA hydratase, but the problem is solved by the action of **2,4-dienoyl-CoA reductase**, followed by enoyl-CoA isomerase; this combination yields the substrate with a Δ^2-*trans* double bond.

untranscribed spacer a region of genomic DNA, lying between genes or groups of genes, that is not transcribed. *See* **spacer** (def. 1).

untranslated region any part of an mRNA molecule not coding for a protein; e.g. in eukaryotes the **poly(A) tail**.

unwinding protein any of the proteins concerned in DNA replication that have a higher affinity for single-stranded DNA than for double-stranded DNA and act to hold the strands apart during replication.

UPA *abbr. for* urokinase-type plasminogen activator; *see* **plasminogen activator**.

U5′pp1Gal *symbol for* uridinediphosphogalactose (alternative to Urd*PP*Gal *or* Urd-5′*PP*-Gal).

U5′pp1Glc *symbol for* uridinediphosphoglucose (alternative to Urd*PP*Glc *or* Urd-5′*PP*-Glc).

up-promoter a mutation that increases **promoter** strength in the expression of a gene.

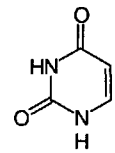
upsilon *symbol*: υ (lower case) *or* Υ (upper case); the twentieth letter of the Greek alphabet.

upstream in or towards positions in a DNA molecule lying in the 5′ direction relative to the start of transcription of a gene.

Ur *or* **UR** *abbr. for* uridine (the symbol Urd is recommended).

Ura *symbol for* a residue of the pyrimidine base **uracil**.

uracil *symbol*: U *or* Ura ; 2,4-dioxopyrimidine; 2,4-pyrimidinediol; one of the pyrimidine bases occurring in RNA (but not in DNA).



uracil

uracil-DNA *N*-glycosylase an enzyme (sub-subclass EC 3.2.2) that removes from DNA any uracil resulting from misincorporation of dUTP that has escaped the action of dUTPase (EC 3.6.1.23, dUTP pyrophosphatase). The enzyme hydrolyses the bond at C-1 of the deoxyribose to yield free uracil and DNA containing an apyrimidinic site; another enzyme, apyrimidine endonuclease, recognizes this site and cleaves the phosphodiester bond on the 5′ side of the deoxyribose moiety. Uracil-DNA *N*-glycosylase may represent the evolutionary basis for the presence of T (not U) in DNA. Cytosine deamination leads to U residues, which would generate transition mutations on replication. In *Escherichia coli* the enzyme is the product of the *ung* gene and mutations in this can be used in certain forced site-directed mutagenesis protocols. The enzyme is a monomer, and is highly conserved in all species. Example, the product of the *ung* gene: database code UNG_ECOLI, 228 amino acids (25.53 kDa).

urate oxidase EC 1.7.3.3; *systematic name*: urate:oxygen oxidoreductase; *other name*: uricase. An enzyme that catalyses the reaction: urate + O_2 → intermediate(s) that lead(s) to **allantoin**. It is a conserved (five motifs) peroxisomal enzyme and a copper protein. Some mammals (e.g. humans, gorillas, etc.) that lack the enzyme are prone to **gout**. Example from rat: database code URIC_RAT, 302 amino acids (34.76 kDa).

Urd *symbol for* a residue of the ribonucleoside **uridine** (alternative to U).

Urd*P* *symbol for* any uridine phosphate.

Urd2′*P* *symbol for* uridine 2′-phosphate.

Urd-2′3′-*P* *symbol for* uridine 2′,3′-phosphate.

Urd3′*P* *symbol for* uridine 3′-phosphate.

Urd-3′5′-*P* *symbol for* uridine 3′,5′-phosphate.

Urd5′*P* *symbol for* uridine 5′-phosphate.

Urd5′*PP* *symbol for* uridine 5′-diphosphate (alternative to ppU).

Urd*PP*Gal *or* **Urd-5′*PP*-Gal** *symbol for* uridinediphosphogalactose (alternatives to U5′pp1Gal).

Urd*PP*Glc *or* **Urd-5′*PP*-Glc** *symbol for* uridinediphosphoglucose (alternatives to U5′pp1Glc).

Urd5′*PPP* *symbol for* uridine 5′-triphosphate (alternative to pppU).

urea the water-soluble compound $H_2N–CO–NH_2$, produced in the liver via the **ornithine–urea cycle**. It is the main nitrogen-containing (urinary) excretion product in **ureotelic** animals. It is used as source of nonprotein nitrogen in ruminant livestock feeds.

urea cycle *see* **ornithine–urea cycle**.

urease EC 3.5.1.5; *systematic name*: urea amidohydrolase; a nickel-protein enzyme that catalyses the hydrolysis of urea to carbon dioxide and ammonia. A carbamoylated lysine provides an oxygen ligand to each nickel, thus explaining a requirement for CO_2 as an activator of urease apoenzyme. Example from *Proteus vulgaris*; a decamer of three subunits (probably in two $\alpha\beta_2\gamma_2$ complexes); α subunit: database code URE1_PROVU, 567 amino acids (60.86 kDa); β subunit: database code URE2_PROVU, 108 amino acids (12.14 kDa); γ subunit: database code URE3_PROVU, 100 amino acids (10.94 kDa). The 3-D structure is known for the *Klebsiella aerogenes* enzyme.

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ureido the NH_2–CO–NH– group, derived from urea by loss of a hydrogen atom.

ureidosuccinase EC 3.5.1.7; an enzyme that hydrolyses *N*-carbamoyl-L-aspartate (ureidosuccinate) to L-aspartate, CO_2, and NH_3.

ureogenic describing an organism (or species) that possesses the full complement of **ornithine–urea cycle** enzymes, and that potentially, but not necessarily, can biosynthesize significant amounts of urea.

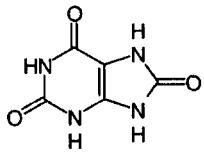
ureosmotic describing an organism (or species) that adjusts urea production or retention in a manner that assists the maintenance of osmotic equilibrium, rather than as a means of disposing of surplus nitrogen.

ureotelic describing an organism (or species) in which **urea** is the principal end product of the degradation of nitrogen-containing compounds. Mammals and marine fishes are typically ureotelic.

Urey, Harold Clayton (1893–1981), US physical chemist; Nobel Laureate in Chemistry (1934) 'for his discovery of heavy hydrogen'.

+uria *comb. form* signifying (in relation to a substance specified) presence unusually, or at a supranormal concentration, in urine. Hence also used to denote a morbid condition so marked, e.g. **phenylketonuria**.

uric acid 2,6,8-trioxypurine; purine-2,6,8-triol; the end product of purine metabolism in certain mammals (including humans) and the main nitrogenous excretory product in **uricotelic** animals. It is formed from xanthine by **xanthine oxidase**. Uric acid is very sparingly soluble in water, and crystalline deposits of monosodium urate occur in the tissues of humans affected by gout.

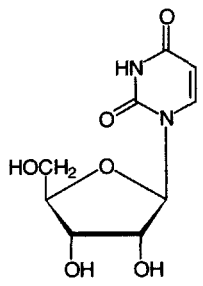


uricase *an alternative name for* **urate oxidase**.

uricosuric (of a drug) tending to promote urinary excretion of uric acid.

uricotelic describing an organism (or species) in which uric acid is the principal end product of the degradation of nitrogen-containing compounds. Uricotelic animals include birds, terrestrial reptiles, and insects. The low solubility of uric acid in water means that it is present as a solid in the excreta of these animals, enabling excretion with little water loss.

uridine *symbol*: U *or* Urd; uracil riboside; 1-β-D-ribofuranosyluracil; a ribonucleoside very widely distributed but occurring almost entirely as phosphoric esters in ribonucleotides and ribonucleic acids. *Compare* **pseudouridine**.

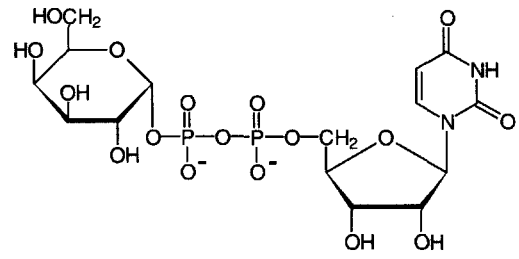


uridine 2′,3′-(cyclic)phosphate *see* **uridine phosphate**.

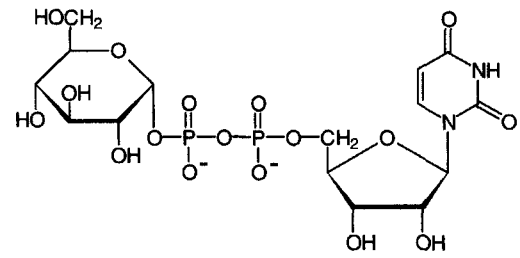
uridine 3′,5′-(cyclic)phosphate *or* **uridine 3′,5′-cyclophosphate** *see* **uridine 3′,5′-phosphate**.

uridine 5′-diphosphate *symbol*: Urd5′*PP or* ppU; *the recommended name for* uridine diphosphate (*abbr.*: UDP); 5′-diphosphouridine; 5′-diphosphouridine; 5′-uridylyl phosphate; uridine 5′-(trihydrogen diphosphate); a universally distributed nucleotide that occurs both in the free state and as a component of a number of important **uridinediphosphosugars**. It is the intermediate in the formation of uridine 5′-triphosphate, UTP, from uridine 5′-phosphate, UMP.

uridine diphosphate galactose *symbol*: Urd-5′-*PP*-Gal *or* U5′pp1Gal *or* UDPGal; uridine 5′-(α-D-galactopyranosyl diphosphate); *recommended name*: uridine(5′)diphospho(1)-α-D-galactose; an important intermediate in the metabolism of D-galactose and in the formation of numerous derivatives. It is formed by the reaction of galactose 1-phosphate with UDP-glucose (catalysed by **uridylyl transferase**), or with UTP (catalysed by **UTP–hexose-1-phosphate uridylyltransferase**).



uridine diphosphate glucose *symbol*: Urd-5′-*PP*-Glc *or* U5′pp1Glc *or* UDPGlc *or* UDPG; uridine 5′-(α-D-glucopyranosyl diphosphate); *recommended name*: uridine(5′)diphospho(1)-α-D-glucose; an important intermediate in the formation of other sugars from glucose. It is formed by the reaction of glucose 1-phosphate with UTP, catalysed by **UTP–glucose-1-phosphate uridylyltransferase**.



uridinediphosphosugar *abbr.*: UDPsugar; *the recommended name for* **uridine diphosphate sugar**; any of many **nucleoside-diphosphosugars** in which the distal phosphoric residue of uridine 5′-diphosphate is in glycosidic linkage with a monosaccharide (or a derivative of a monosaccharide). UDPsugars are particularly important as coenzymes for many types of reaction involving the transfer of monosaccharide residues in the biosynthesis of oligosaccharides and polysaccharides (especially in plants) and in the formation of the oligosaccharide moieties of **glycoconjugates**. The main UDPsugars in this category are: UDP-L-arabinose, UDP-D-galactose (*see* **uridine diphosphate galactose**), UDP-D-galacturonate, UDP-D-glucose (*see* **uridine diphosphate glucose**), UDP-D-glucuronate, and UDP-D-xylose, all of which are (directly or indirectly) inter-

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convertible where they occur together; UDP-L-iduronate, which is formed by epimerization of UDP-D-glucuronate; UDP-*N*-acetyl-D-galactosamine and UDP-*N*-acetyl-D-glucosamine, which are interconvertible; and UDP-*N*-acetylmuramate, which is synthesized from UDP-*N*-acetyl-D-glucosamine. In addition, certain UDPsugars, particularly UDP-D-glucose and UDP-D-glucuronate, are coenzymes for the formation in animals or plants of glycosides with a variety of aglycons such as bilirubin, phenols, plant pigments and sterols, and steroid hormones.

uridine kinase EC 2.7.1.48; *other name*: uridine monophosphokinase; an enzyme that catalyses the phosphorylation by ATP of uridine to uridine 5′-phosphate with formation of ADP. Example from yeast: database code URK1_YEAST, 501 amino acids (56.23 kDa).

uridine monophosphate *abbr.*: UMP; *an alternative name for* any uridine phosphate, but in particular for uridine 5′-phosphate, especially when its distinction from uridine (5′-)diphosphate and uridine (5′-)triphosphate requires emphasis.

uridine 5′-monophosphate synthase *abbr.*: UMP synthase; a multifunctional enzyme that in higher eukaryotes carries out the following two reactions: (1) orotate phosphoribosyltransferase, EC 2.4.2.10; *other names*: orotidylic acid phosphorylase, orotidine-5′-phosphate pyrophosphorylase; *systematic name*: orotidine-5′-phosphate:pyrophosphate phospho-α-D-ribosyltransferase; a reaction of the pathway for *de novo* biosynthesis of pyrimidine nucleotides. It catalyses a reaction between orotate and 5-phospho-α-D-ribose 1-diphosphate to form orotidine 5′-phosphate and pyrophosphate. (2) orotidine-5′-phosphate decarboxylase, EC 4.1.1.23; *systematic name*: orotidine-5′-phosphate carboxy-lyase; a decarboxylation reaction that forms uridine 5′-monophosphate and CO_2 from orotidine 5′-phosphate. Example from *Bos taurus*: database code PYR5_BOVIN, 480 amino acids (52.23 kDa).

uridine phosphate *symbol*: Urd*P*; uridine monophosphate (*abbr.*: UMP); any phosphoric monoester or diester of uridine. There are three monoesters – uridine 2′-phosphate, uridine 3′-phosphate, and **uridine 5′-phosphate** – and two diesters – uridine 2′,3′-phosphate and **uridine 3′,5′-phosphate** – although uridine 5′-phosphate is the ester commonly denoted (the locant being omitted if no ambiguity may arise). Uridine 2′,3′-phosphate (*symbol*: Urd-2′,3′-*P*), *also named* uridine 2′,3′-(cyclic)phosphate *or* cyclic uridine 2′,3′-monophosphate (*abbr.*: 2′,3′-cyclic UMP), is formed as an intermediate during the alkaline hydrolysis of ribonucleic acid. This diester then readily hydrolyses to a mixture of the two monoesters uridine 2′-phosphate (*symbol*: Urd2′*P*), *also named* uridine 2′-monophosphate (*abbr.*: 2′UMP) *or* 2′-uridylic acid *or* uridylic acid a, and uridine 3′-phosphate (*symbol*: Urd3′*P*), *also named* uridine 3′-monophosphate (*abbr.*: 3′UMP) *or* 3′-uridylic acid *or* uridylic acid b.

uridine 2′-phosphate *see* **uridine phosphate**.

uridine 2′,3′-phosphate *see* **uridine phosphate**.

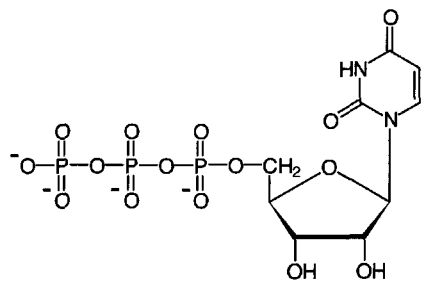
uridine 3′-phosphate *see* **uridine phosphate**.

uridine 3′,5′-phosphate *symbol*: Urd-3′,5′-*P*; *the recommended name for* cyclic uridine 3′,5′-monophosphate (*abbr.*: 3′,5′-cyclic UMP *or* cyclic UMP *or* cUMP); uridine 3′,5′-cyclophosphate; uridine 3′,5′-(cyclic)phosphate; a monophosphoric diester of uridine found in practically all mammalian tissues. It is a cyclic nucleotide similar in structure and metabolism to **adenosine 3′,5′-phosphate**, cyclic AMP. It has been reported to inhibit the growth of certain transplantable tumours.

uridine 5′-phosphate *or* **5′-uridylic acid** *or* **5′-phosphouridine** *or* **5′-*O*-phosphonouridine** *symbol*: Urd5′*P*; *alternative recommended names for* uridine 5′-monophosphate (*abbr.*: 5′UMP); uridine 5′-(dihydrogen phosphate); uridine (mono)ribonucleotide. (The locant is commonly omitted if there is no ambiguity as to the position of phosphorylation). It is biosynthesized from aspartate, the last stage of the reaction sequence being the decarboxylation of orotidine 5′-phosphate, orotidylic acid. In addition, resynthesis of UMP from free uridine formed by degradation of ribonucleic acid can be effected via a **salvage pathway**. UMP is a key intermediate in the formation of uridine 5′-triphosphate, UTP, and hence in the biosynthesis of other pyrimidine nucleotides.

uridine phosphorylase *see* **pyrimidine-nucleoside phosphorylase**.

uridine 5′-triphosphate *symbol*: Urd5′*PPP or* pppU; *the recommended name for* uridine triphosphate (*abbr.*: UTP); 5′-triphosphouridine; 5′-uridylyl diphosphate; uridine 5′-(tetrahydrogen triphosphate); an important nucleotide present in all cells. It is formed from uridine 5′-phosphate via uridine 5′-diphosphate by the successive action of nucleoside-phosphate kinase (EC 2.7.4.4) and nucleoside-diphosphate kinase (EC 2.7.4.6), which transfer in turn the terminal phosphoric residues from two molecules of adenosine 5′-triphosphate. UTP is the starting point for the biosynthesis, first of cytidine triphosphate, next of cytidine diphosphate, and then, in a succession of further reactions, of various deoxyribonucleotides of cytosine, uracil, and thymine. It is important also for the formation of uridinediphosphogalactose and uridinediphosphoglucose through the action of certain **uridylyltransferases**, and thence of a number of other uridinediphosphosugars.



uridyl **1** any chemical group formed by the loss of a 2′-, a 3′-, or a 5′-hydroxyl group from the ribose moiety of uridine. **2** *a misnomer for* **uridylyl**.

uridylate **1** either the monoanion or the dianion of uridylic acid. **2** any mixture of uridylic acid and its anions. **3** any salt or ester of uridylic acid.

uridylic acid *the trivial name for* any phosphoric monoester of uridine. The position of the phosphoric residue on the ribose moiety of a given ester may be specified by a prefixed locant; *see* **uridine phosphate**. However, 5′-uridylic acid is the ester commonly denoted, its locant usually being omitted if no ambiguity may arise. 5′-Uridylic acid is also an alternative recommended name for **uridine 5′-phosphate**.

uridyl transferase *another name for* **UDPglucose–hexose-1-phosphate uridylyltransferase**. This is a misnomer; *compare* **uridyl** *with* **uridylyl**.

uridylyl the uridine[mono]phospho group; the acyl group derived from uridylic acid. *Distinguish from* **uridyl**.

uridylylate to introduce uridylyl groups into a compound (e.g. a protein, a ribonucleic acid, or a sugar phosphate), generally through the action of a uridylyltransferase. —**uridylylated** *adj.*; **uridylylation** *n.*

uridylyl-removing enzyme *the provisional name for* a putative enzyme present in *Escherichia coli* that detaches uridylyl groups from uridylylated nitrogen regulatory protein P_{II} by hydrolysis, with formation of uridylate. *See also* **nitrogen regulatory protein**, **uridylyltransferase**.

uridylyltransferase EC 2.7.7.12; *recommended name*: UDPglucose–hexose-1-phosphate uridylyltransferase; *systematic name*: UDPglucose:α-D-galactose-1-phosphate uridylyltransferase; *other names*: uridylyl removing enzyme; P_{II} uridylyl-transferase. An enzyme that catalyses the reaction:

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UDPglucose + α-D-galactose 1-phosphate = α-D-glucose 1-phosphate + UDPgalactose.

The *Escherichia coli* enzyme comprises 890 amino acids (102.31 kDa) and modifies the **nitrogen regulatory protein P_{II}**.

urinalysis the chemical and physical analysis of urine.

urinary of, or pertaining to, urine.

urinary stone protein *see* **osteopontin**.

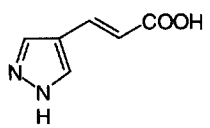
urine the aqueous excretion produced by the kidneys in higher animals. It serves as a vehicle for the elimination of certain metabolic waste products, e.g. **urea** and **uric acid**, and for the removal of excess ions and water. In mammals and fishes it is fluid, while in birds and reptiles it is semi-solid.

urinometer a **hydrometer** specifically designed and calibrated for measuring the specific gravity of (mammalian) urine.

urobilin *or* **urobilin IXα** a yellow coloured linear tetrapyrrole. It is formed in kidney and is an oxidation product of **urobilinogen**; the central methylene group linking pyrrole units has been converted to –CH=. Urobilin gives urine its characteristic yellow colour. *See also* **stercobilin**.

urobilinogen *or* **mesobilirubinogen** *or* **urobilinogen IXα** a colourless linear tetrapyrrole formed in heme catabolism. It arises by reduction of free **bilirubin** released from its glucuronide by intestinal bacterial hydrolases. The four pyrrole rings are linked by three methylene groups. *See also* **stercobilinogen**.

urocanoate 4-imidazoleacrylate; 3-(1*H*-imidazol-4-yl)propenoate: an intermediate in the degradation of L-histidine, from which it is formed through the action of **histidine ammonia-lyase** by elimination of ammonium.



urocanic acid

urodilatin a 32-amino-acid peptide, isolated from human urine that is identical in sequence to human **natriuretic peptide** (ANP) but with an N-terminal Thr-Ala-Pro-Arg tetrapeptide extension. It has actions similar to ANP.

uroflavin *or* **uroflavine** *a former name for* **riboflavin**.

urogastrone a name given (by analogy with **enterogastrone**) to a proteinaceous agent present in human urine that potently inhibits gastric secretion. It is now believed to be identical or nearly identical with human **epidermal growth factor**.

urokinase a proteolytic enzyme found in urine, blood, and kidney cells, that converts **plasminogen** to **plasmin**. *See* **plasminogen activator**.

uromodulin *another name for* **Tamm–Horsfall glycoprotein**.

uronate **1** the anion of uronic acid. **2** any mixture of a uronic acid and its anion. **3** any salt or ester of a uronic acid.

uronic acid any monocarboxylic acid formally derived by oxidizing to a carboxyl group the terminal hydroxymethylene group either of an **aldose** having four or more carbon atoms in the molecule, or of any glycoside derived from such an aldose. The carbon atom of the (potential) aldehydic carbonyl group is numbered C-1.

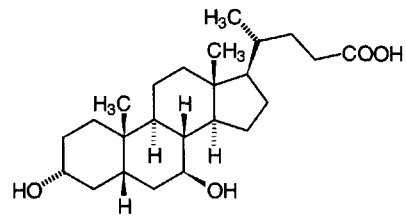
uropontin *see* **osteopontin**.

uroporphyrin-III *C*-methyltransferase EC 2.1.1.107; *systematic name*: *S*-adenosyl-L-methionine:uroporphyrin-III *C*-methyltransferase (*abbr.*: SUMT); *other names*: urogen-III methylase; uroporphyrin-III methylase. An enzyme that catalyses a reaction between two molecules of *S*-adenosyl-L-methionine and uroporphyrin III to form two molecules of *S*-adenosyl-L-homocysteine and sirohydrochlorin. It is a component of **siroheme synthase**, and effects a step in the biosynthesis of siroheme and cobalamin.

uroporphyrinogen decarboxylase EC 4.1.1.37; *systematic name*: uroporphyrinogen-III carboxy-lyase. An enzyme that catalyses the decarboxylation of uroporphyrinogen-III to coproporphyrinogen with loss of four molecules of CO_2; this is a step in the pathway of heme synthesis, whereby the four carboxymethyl groups of uroporphrinogen are converted to methyl groups. Example from yeast: database code DCUP_YEAST, 362 amino acids (41.30 kDa).

uroporphyrinogen-III synthase EC 4.2.1.75; *systematic name*: hydroxymethylbilane hydro-lyase (cyclizing); *other names*: uroporphyrinogen-III cosynthetase; uroporphyrinogen-III cosynthase. An enzyme that catalyses the conversion of hydroxymethylbilane to uroporphyrinogen-III and H_2O. Example from *Escherichia coli*: database code HEM4_ECOLI, 246 amino acids (27.77 kDa).

ursodeoxycholate 3α,7β-dihydroxy-5β-cholan-24-oate; an epimer of **chenodeoxycholate** found in the bile of bears (hence the name, from Ursidae), as a conjugate with taurine. Used therapeutically, it prevents the synthesis and absorption of cholesterol and can lead to the dissolution of gallstones.



U-snRNA *abbr. for* uridylate-rich small nuclear RNA; a family of snRNA molecules, often designated U1 to U6 snRNA, that contain 100–215 nucleotides and a 'capped' 5′ end. They usually occur in combination with proteins as small nuclear ribonucleoprotein particles. Their function is unclear, but may be related to splicing heterogeneous nuclear RNA (hnRNA) to mature mRNA.

USP *abbr. for* United States Pharmacopeia.

USPHS *abbr. for* United States Public Health Service.

uterine metalloendopeptidase *see* **matrilysin**.

uteroglobin *or* **blastokinin** a protein regulator of progesterone concentrations reaching the blastocyst and a potent inhibitor of phospholipase A_2. It is a disulfide-linked homodimer. Example (precursor) from *Oryctolagus cuniculus*: database code UTER_RABIT, 91 amino acids (9.97 kDa).

uterus (*pl.* **uteri**) a muscular part of the reproductive tract of female mammals (except Monotremata) that contains the developing embryo and fetus during pregnancy. —**uterine** *adj.*

UTP *abbr. for* uridine (5′-)triphosphate.

UTP–glucose-1-phosphate uridylyltransferase EC 2.7.7.9; *systematic name*: UTP:α-D-glucose-1-phosphate uridylyltransferase; *other names*: UDPglucose pyrophosphorylase; glucose-1-phosphate uridylyltransferase; one of the enzymes that can form uridinediphosphoglucose. It catalyses a reaction between UTP and α-D-glucose 1-phosphate to form UDPglucose and pyrophosphate. Example from *Escherichia coli*: database code GALU_ECOLI, 302 amino-acid residues (32.90 kDa).

UTP–hexose-1-phosphate uridylyltransferase EC 2.7.7.10; *systematic name:* UTP:α-D-hexose-1-phosphate uridylyltransferase; one of the enzymes that can form uridinediphosphogalactose. It catalyses a reaction between UTP and α-D-galactose 1-phosphate to form UDPgalactose and pyrophosphate. α-D-Glucose 1-phosphate can also act (but more slowly) as an acceptor, forming uridinediphosphoglucose. Example from human; database code GAL7_HUMAN, 379

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amino acids (43.16 kDa). The absence of the enzyme in infancy causes a mild form of **galactosemia**.

UTP–xylose-1-phosphate uridylyltransferase EC 2.7.7.11; *other name*: xylose-1-phosphate uridylyltransferase; an enzyme that catalyses a reaction between UTP and α-D-xylose 1-phosphate to form UDPxylose and pyrophosphate.

utrophin *or* **dystrophin-related protein** (*abbr.*: DRP) a protein that is highly homologous to **dystrophin** and found in normal adult human muscle, primarily at the neuromuscular junction. In the absence of dystrophin in Duchenne muscular dystrophy it is also present in the sarcolemma. It is an actin-binding protein related to α-**actinin**. Both gene and protein sequences resemble those for dystrophin. Overexpression of utrophin in a dystrophin-deficient (*mdx*) mouse demonstrates that it can functionally replace dystrophin; it has been suggested that this could offer a therapeutic strategy for Duchenne muscular dystrophy. Example from human: database code S28381, 3433 amino acids (394.05 kDa).

UUA a codon in mRNA for L-leucine.

UUC a codon in mRNA for L-phenylalanine.

UUG a codon in mRNA for L-leucine.

UUU a codon in mRNA for L-phenylalanine.

UV *or* **uv** *abbr. for* ultraviolet (radiation).

uvomorulin *or* **epithelial cadherin** *or* **E-cadherin** a type I membrane protein and **cadherin** of non-neural epithelial tissues.

uvr any of four genes in *Escherichia coli* that are induced by the **SOS repair** system and whose products are involved in the repair of damage to DNA caused by UV light and DNA-reactive chemicals. Three of these genes, *uvrA*, *uvrB*, and *uvrC*, encode the three subunits of the ABC excision nuclease; this recognizes the structural distortion created by a **thymine dimer** and cleaves the damaged strand at two sites, leaving a gap that is subsequently filled by polymerase and ligase action. Because the enzyme cuts at two sites it is not a classical endonuclease, but is referred to as an **excinuclease**. The fourth gene, *uvrD*, encodes a DNA helicase with ATPase activity, similar to the *rep* (*see* **RepA**) gene product; it promotes the ATP-dependent unwinding of the DNA duplex during repair; example, database code UVRD_ECOLI, 720 amino acids (81.90 kDa).

UWGCG *abbr. for* University of Wisconsin Genetics Computer Group. *See* **GCG**.

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Vv

v *symbol for* **1** specific volume. **2** volume (alternative to *V*). **3** velocity of reaction (i.e. **rate of reaction**); a subscript (in small capital letters) may be added (e.g. v_A) to denote rate of consumption, or rate of formation, of a specified reactant (e.g. A). **4** initial velocity of an enzymic reaction; *see also* v_0. **5** (bold italic) velocity (alternative to *u*, *w*, or *c*).

v_0 *symbol for* initial velocity (i.e. initial rate) of an enzymic reaction. The subscript may be omitted when rates at other times are not in question.

v_i *symbol for* chemical flux through the (enzymic) step with rate constant k_i. Similarly, flux through steps with rate constants k_{-i} or k_{ij} are denoted by v_{-i} and v_{ij} respectively.

v_{max} *symbol for* the true maximum value of the **rate of reaction**. *Compare* V_{max}.

V *symbol for* **1** volt. **2** a residue of the α-amino acid L-valine (alternative to Val). **3** vanadium. **4** variable region (of an immunoglobulin chain).

V *symbol for* **1** electric potential. **2** potential energy. **3** volume (alternative to *v*). **4** maximum velocity (i.e. **limiting rate**, or maximum rate) of an enzymic reaction (alternative to V_{max}).

V_m *symbol for* molar volume.

V_M *symbol for* hold-up volume.

V_{max} *symbol for* maximum velocity (i.e. **limiting rate**) of an enzyme reaction (alternative to *V*).

Vac *symbol for* vaccenic acid.

vaccenate **1** *numerical symbol*: 18:1(11); *the trivial name for* either of the isomers (*cis*-vaccenate and *trans*-vaccenate) of octadec-11-enoate, $CH_3–[CH_2]_5–CH=CH–[CH_2]_9–COO^-$, the anions derived from *cis*-vaccenic acid, (*Z*)-octadec-11-enoic acid, and *trans*-vaccenic acid, (*E*)-octadec-11-enoic acid, a stereoisomeric pair of monounsaturated straight-chain higher fatty acids. *See also* **octadecenoic acid**. **2** any mixture of either *cis*- or *trans*-vaccenic acid and its corresponding anion. **3** any salt or ester of either isomer of vaccenic acid.

vaccenoyl *symbol*: Vac; *the trivial name for* either of the isomers (*cis*-vaccenoyl and *trans*-vaccenoyl) of octadec-11-enoyl, $CH_3–[CH_2]_5–CH=CH–[CH_2]_9–CO–$, the acyl groups derived from *cis*-vaccenic acid, (*Z*)-octadec-11-enoic acid, and *trans*-vaccenic acid, (*E*)-octadec-11-enoic acid. The *cis*-vaccenoyl group is a major fatty-acyl component of many bacterial lipids and a constituent of the oils of marine organisms. The *trans*-vaccenoyl group is present in a minor proportion of the acylglycerols in the body and milk fats of ruminants.

vaccination the process of administering a **vaccine** to produce immunity.

vaccine any preparation of immunogenic material suitable for the stimulation of active immunity in animals without inducing disease. Vaccines may be based on dead or attenuated microorganisms; altered toxins (toxoids); or viruses.

vaccinia virus a DNA virus and the type species of the genus *Orthopoxvirus* (or 'vaccinia subgroup'), which also includes the viruses responsible for cowpox, buffalopox, catpox, mousepox, and (formerly) smallpox (variola virus). Vaccinia infection usually causes only mild symptoms. Because of its serological similarity to the smallpox virus, vaccinia virus was formerly used as the basis of a live vaccine to protect humans against smallpox. Viral antigens are often on the surface of virus particles, and some of these antigens can be engineered into the coat of vaccinia. For example, engineered vaccinias with surface antigens of hepatitis B, influenza virus, and vesicular stomatitis virus (which kills cattle, horses, and pigs) have produced useful vaccines in animal tests. However, the known adverse reactions with vaccinia-virus vaccines are well documented and their incidence and severity must be carefully weighed.

vacuolar apparatus the cellular digestive system, consisting of **lysosomes** and closely related, hydrolase-free, vacuolar structures. It is concerned with the digestion of both endogenous and exogenous materials.

vacuolar ATPase an enzyme of the synaptic vesicle membrane that pumps protons into the vesicle as it loses acetylcholine during nerve transmission; subsequently, the hydrons are released as the vesicle is recharged with acetylcholine. The enzyme (at least 10 subunits) resembles **H^+-transporting ATP synthase**, but functions as a proton pump. Example from bovine: database code VATA_BOVIN, 617 amino acids (68.31 kDa). The catalytic subunits are highly conserved; e.g. the enzyme from carrot comprises 623 amino acids (68.76 kDa).

vacuole a closed structure, found only in eukaryotic cells, that is completely surrounded by unit membrane and contains liquid material. *Compare* **vesicle**.

vacuum (*pl.* **vacuums** *or* **vacua**) a space containing a gas at low pressure; i.e. a space in which there are relatively few atoms or molecules. A **perfect vacuum** would contain no atoms or molecules, but this is unobtainable owing to the vapour pressure of materials containing any vaccum. Vacuums may be classified into **low** (or **soft**) **vacuum**, $>\approx 10^{-2}$ Pa; **high** (or **hard**) **vacuum**, 10^{-2}–10^{-7} Pa; and **ultrahigh vacuum**, $<10^{-7}$ Pa.

vacuum evaporation a technique for depositing a thin film of some solid material on a surface by evaporating the material at a high temperature in a vacuum. Atoms leaving the hot material travel directly to the cool surface to form a coating without colliding with other molecules in the gas phase; they condense on the cool surface and build up a layer of solid. *See also* **shadow casting**.

vacuum ultraviolet *see* **ultraviolet radiation**.

vagusstoff *the German name for* 'active factor'. The existence of such a factor was first demonstrated by **Loewi** (1903); it was secreted into plasma after stimulation of the vago-sympathetic trunk, and was found to inhibit cardiac function. It was later identified by **Dale** as **acetylcholine**.

Val *symbol for* **1** the α-amino acid L-valine (alternative to V). **2** the (*cis*- or *trans*-) vaccenoyl group.

valency *or (esp. US)* **valence** **1** the numerical combining power of an atom (and thus of a chemical element), ion, or chemical group, equal to the number of hydrogen atoms that the atom, ion, or group could combine with or replace. *See also* **covalence**, **electrovalence**. **2** the number of antigenic determinants with which one antibody molecule, or fragment thereof, will combine.

valerate **1** *the trivial and preferred name for* pentanoate; the anion, $CH_3–[CH_2]_3–COO^-$, derived from valeric acid (i.e. pentanoic acid). **2** any mixture of free valeric acid and its anion. **3** any salt or ester of valeric acid.

valeryl *symbol*: Vl; *the trivial and preferred name for* pentanoyl; the acyl group, $CH_3–[CH_2]_3–CO–$, derived from valeric acid (i.e. pentanoic acid).

valinate **1** valine anion; the anion, $(CH_3)_2CH–CH(NH_2)–COO^-$, derived from **valine**. **2** any salt containing valine anion. **3** any ester of valine.

valine *the trivial name for* α-aminoisovaleric acid; α-amino-β-methylbutyric acid; 2-amino-3-methylbutanoic acid; $(CH_3)_2CH–CH(NH_2)–COOH$; a chiral α-amino acid. L-valine (*symbol*: V *or* Val), (*S*)-2-amino-3-methylbutanoic acid, is a coded amino acid found in peptide linkage in proteins; codon: GUA, GUC, GUG, or GUU. In mammals it is an essential dietary amino acid and is glucogenic. Residues of D-valine (*symbol*: D-Val *or* DVal), (*R*)-2-amino-3-methylbutanoic acid, occur in a number of peptide antibiotics, e.g. several members of the actinomycin family, gramicidins A, B, C, and D, and valinomycin (the latter also contains residues of L-valine). (Illustrated overleaf).

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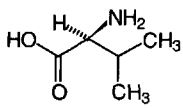

L-valine

valine–isoleucine aminotransferase *see* **valine–3-methyl-2-oxovalerate aminotransferase**.

valine–3-methyl-2-oxovalerate aminotransferase EC 2.6.1.32; *recommended name*: valine–3-methyl-2-oxovalerate transaminase; *other names*: valine–isoleucine transaminase; valine–isoleucine aminotransferase; an enzyme that catalyses the reaction:

L-valine + (*S*)-3-methyl-2-oxopentanoate = 3-methyl-2-oxobutanoate + L-isoleucine.

See also **transamination**.

valinium valine cation; the cation $(CH_3)_2CH–CH(NH_3^+)–COOH$, derived from **valine**.

valino the alkylamino group, $(CH_3)_2CH–CH(COOH)–NH–$, derived from **valine**.

valinomycin a cyclic 12-residue depsipeptide antibiotic that consists of three moieties, each having one molecule each of L-valine, D-α-hydroxyvaleric acid, D-valine, and L-lactic acid. The linkage from the D-valine carboxyl group is directly onto the α-carbon of L-lactic acid. Valinomycin is produced by *Streptomyces fulvissimus*. It is active especially against *Mycobacterium tuberculosis*. It can act as an ionophore, the molecule being folded to produce a hydrophobic surface with an interior that binds a univalent cation such as Rb^+, Cs^+, NH_4^+, or, especially, K^+. This property equips valinomycin to interfere with oxidative phosphorylation by rendering the mitochondrial membrane permeable to K^+ ions.

valium *see* **diazepam**.

valproic acid 2-propylpentanoic acid; $(CH_3–CH_2–CH_2)_2CH–COOH$; an antiepileptic, also used as the sodium salt, sodium valproate (*one proprietary name*: Epilim).

valyl the acyl group, $(CH_3)_2CH–CH(NH_2)–CO–$, derived from **valine**.

VAMP *abbr. for* vesicle-associated membrane protein; *another name for* **synaptobrevin**.

vancomycin a complex glycopeptide, $C_{66}H_{75}Cl_2N_9O_{24}$, from *Streptomyces orientalis*. It inhibits a specific step in the synthesis of the peptidoglycan layer in the Gram-positive bacterium *Staphylococcus aureus*. *See also* **vancosamine**.

vancosamine the aminodeoxysugar 3-amino-2,3,6-trideoxy-3-*C*-methyl-L-*lyxo*-hexose; the carbohydrate component of **vancomycin**.

van den Bergh reaction a colorimetric reaction for the determination of **bilirubin** that depends on the formation of a red azo dye by bilirubin and diazotized sulfanilic acid. A **direct van den Bergh reaction** in aqueous solution is given by bilirubin glucuronide, and an **indirect van den Bergh reaction** is given in alcoholic solution by free bilirubin. [After A. A. Hijmans van den Bergh (1869–1943), Dutch physician.]

van der Waals forces long-range forces between molecules or submolecular groups, effective from >50 nm to interatomic spacings. They are always present, albeit rather weak, but often compete with electrostatic forces. In general the van der Waals forces do not follow a simple power law; e.g. the force may be attractive at large separations but repulsive at small ones, or vice versa. The van der Waals free energy between two molecules or submolecular groups usually depends on their mutual orientation, i.e. these forces tend to align two molecules so as to minimize their free energy of interaction. [After Johannes Diderik van der Waals (1837–1923), Dutch physicist.]

van der Waals radius one half of the internuclear distance between atoms at equilibrium when the long-range attractive forces balance the short-range repulsive forces. It is larger than the atom's covalent radius and is about equal to the ionic radius of monovalent ions.

Van Dyke protein *an old name for* **neurophysin**.

Vane, (Sir) John Robert (1927–), British pharmacologist; Nobel Laureate in Physiology or Medicine (1982) jointly with S. K. Bergström and B. I. Samuelsson 'for their discoveries concerning prostaglandins and related biologically active substances'.

vanillylmandelate *see* **hydroxy-methoxymandelate**.

van Niel, Cornelius Bernardus (1897–1984), US microbiologist who inherited the traditions of the Delft school; he proposed the general equation for photosynthesis as

$$6\,CO_2 + 12\,H_2A = (CH_2O)_6 + 6\,H_2O + 12\,A.$$

He was renowned for his summer course in microbiology at the Hopkins Marine Station, Pacific Grove, California.

Van Slyke apparatus **1** a volumetric apparatus formerly widely used for the determination of oxygen and carbon dioxide contents of blood samples. **2** an apparatus for the gasometric determination of aliphatic amino-nitrogen, e.g. in proteins, by measurement of the nitrogen gas evolved on reaction with nitrous acid. [After Donald Dexter Van Slyke (1883–1971), US biochemist.]

van't Hoff, Jacobus Henricus (1852–1911), Dutch physical chemist and stereochemist distinguished, *inter alia*, for postulating the tetrahedral disposition of the bonds to a singly bonded carbon atom, for being the first to apply the laws of thermodynamics to chemical reactions, and for showing that osmotic pressure varies directly with absolute (i.e. thermodynamic) temperature; Nobel Laureate in Chemistry (1901) 'in recognition of the extraordinary services he has rendered by the discovery of the laws of chemical dynamics and osmotic pressure in solutions'.

van't Hoff equation *or* **van't Hoff isochore** a relation describing the temperature variation of an equilibrium constant, K, of a reaction in terms of the change in heat content, $\Delta H'$, i.e. in terms of the heat of reaction at constant pressure. It is: $d\ln K/dT = \Delta H/RT^2$, where R is the gas constant and T the thermodynamic temperature.

van't Hoff law the principle that the osmotic pressure exerted by a solute is equal to the pressure the solute would exert if it were an ideal gas at the same temperature as the solution and of the same volume. Hence $\Pi V = RT$, where Π is the osmotic pressure, V is the volume of solution containing 1 mole of solute, R the gas constant, and T the thermodynamic temperature.

van't Hoff limiting law a relation giving the limiting value for the osmotic pressure exerted by an ideal solute:

$$\text{limit } (c \to 0)\ \Pi = RT/M_r,$$

where Π is the osmotic pressure, c the solute concentration, M_r the relative molecular mass of the solute, R the gas constant, and T the thermodynamic temperature.

variable **1** liable to change; having a range of possible values; liable to deviate from an established type. **2** something that is subject to variation; a quantity or function that can assume any of a set of specified values; a symbol for any unspecified number or quantity.

variable arm *an alternative name for* **extra arm** of tRNA.

variable number tandem repeats *abbr.*: VNTR; a multiallelic DNA polymorphism that results from insertions or deletions of DNA between two **restriction sites**. The existence of these repeats is exploited in **genetic profiling**.

variable region *symbol*: V; a region of a chain of an **immunoglobulin** molecule having an amino-acid sequence that characteristically varies between molecules of the same immunoglobulin class. There are typically four variable regions: the N-terminal halves of the two **light chains** (V_L) and the N-terminal halves of the **Fd fragments** (V_H) of the two heavy chains. The amino-acid sequences of these variable regions de-

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termine the structure of the antibody-combining site. *Compare* **constant region**.

variance a measure of the dispersion of a population, the mean square average of the deviations from the **mean**. It is the square of the **standard deviation**, σ, of that population.

variant **1** something that deviates from the norm; used especially of abnormal proteins (e.g. hemoglobins). **2** different; showing variation; used especially of different amino-acid residues in the corresponding positions of polypeptide chains from different sources.

Varmus, Harold Eliot (1939–), US microbiologist and molecular biologist; Nobel Laureate in Physiology or Medicine (1989) jointly with M. J. Bishop 'for their discovery of the cellular origin of retroviral oncogenes'.

vascular of, or relating to vessels that conduct fluid from one part of an organism to another, e.g. the blood vessels in animals, or the xylem and phloem in plants.

vascular cell adhesion molecule *see* **VCAM**.

vascular endothelial growth factor *abbr.*: VEGF; *also known as* **vascular permeability growth factor** *or* **vasculotropin**; a protein that is produced by epithelial cells, macrophages, and smooth muscle cells, and is active in angiogenesis and endothelial cell growth; it induces endothelial proliferation and vascular permeability. Related to **platelet-derived growth factor**, it is a disulfide-linked homodimer. Example (precursor) from human: database code VEGF_HUMAN, 215 amino acids (25.14 kDa).

vascular endothelial growth factor receptor *abbr.*: VEGF receptor; a type I membrane protein of the immunoglobulin superfamily (seven immunoglobulin-fold domains in the extracellular part) found in the lung and elsewhere. It is a tyrosine kinase receptor related to the platelet-derived growth factor receptor, with a nonkinase insert between the kinase domains. Example (precursor of receptor 1) from human: database code VGR1_HUMAN, 1338 amino acids (150.56 kDa).

vascular permeability growth factor *see* **vascular endothelial growth factor**.

vasculature the **vascular** system in animals.

vasculotropin *see* **vascular endothelial growth factor**.

vaso+ *comb. form* denoting a blood vessel.

vasoactive describing any agent that affects the diameter of blood vessels. *See also* **vasoconstrictor**, **vasodilator**.

vasoactive intestinal contractor *see* **endothelin**.

vasoactive intestinal polypeptide *abbr.*: VIP; a basic 28-residue peptide amide, similar in sequence to **gastric inhibitory polypeptide**, **glucagon**, and **secretin**, that is widely distributed in the body, mainly in nervous tissue (especially of the gut) and appears to act as a neurotransmitter in **peptidergic** autonomic nerves. It has a wide range of biological activities, including potent hypotensive and vasodilatory effects. It has the sequence

HSDAVFTDNYTRLRKQMAVKKYLNSILN–NH_2.

vasoactive intestinal polypeptide receptor *or* **vasoactive intestinal peptide receptor** any of a family of proteins that bind **vasoactive intestinal polypeptide** (VIP) and mediate its intracellular effects. The receptor is a G-protein-coupled seven-transmembrane-domain protein (362 residues, human). The effector pathway involves adenylate cyclase activation; other endogenous ligands include peptide HI (PHI), GHRH, and secretin, the order of potency being VIP > PHI > GHRH > secretin.

vasoconstrictor a vasoactive agonist that causes **vasoconstriction**, i.e. a decrease in the diameter of blood vessels.

vasodilator a vasoactive agonist that causes **vasodilation**, i.e. an increase in the diameter of blood vessels.

vasopressin *or* **antidiuretic hormone** (*abbr.*: ADH); either of two nonapeptide hormones secreted by the neurohypophysis and structurally very similar to **vasotocin** and **oxytocin**. **[8-Arginine]vasopressin** (*abbr.*: [Arg^8]vasopressin *or* AVP) has the sequence

Cys-Tyr-Phe-Gln-Asn-Cys-Pro-Arg-Gly-amide,

with a disulfide bridge between the half-cystine residues at positions 1 and 6. It has a pressor action by causing vasoconstriction in the peripheral arterioles and capillaries. It also has an antidiuretic action by accelerating water reabsorption from the proximal region of the distal convoluted tubules of the kidney. AVP is synthesized as part of a large precursor molecule, ***vasopressin–neurophysin 2–copeptin precursor***, which includes its associated carrier protein (**neurophysin**), and is then packaged into granules in which the nonapeptide is formed by proteolytic cleavage. Subsequently it is released, on action of a specific stimulus, into the blood, in which it circulates in unbound form. Deficiency of AVP is the cause of autosomal dominant neurohypophyseal diabetes insipidus (ADNDI). The analogue, [8-lysine]vasopressin (*abbr.*: [Lys^8]-vasopressin), in which lysine is substituted for arginine at position 8, is formed, either singly or together with arginine vasopressin, in the pig family.

vasopressin–neurophysin 2–copeptin precursor the precursor of **vasopressin**, neurophysin 2 (*see* **neurophysin**), and a third peptide, copeptin. Example from human: database code NEU2_HUMAN, 164 amino acids (17.31 kDa). Copeptin is a glycopeptide that contains 38 amino-acid residues forming the third domain of mammalian vasopressin–neurophysin precursor. It is released during intra-axonal processing of the precursor.

vasopressin receptor any of a family of membrane proteins that bind [8-arginine]vasopressin (AVP; *see* **vasopressin**) and mediate its intracellular effects; peptides related to AVP, including **oxytocin**, are also bound. Two types of vasopressin receptor have been defined: V_1 – subdivided into V_{1a} (vascular/hepatic) and V_{1b} (anterior pituitary) – and V_2 (kidney); these can be distinguished pharmacologically on the basis of selective agonists. V_2 receptors are restricted to the kidney and colocalize at the chromosomal locus for **nephrogenic diabetes insipidus**. V_1 receptors are coupled to phosphoinositide-specific phospholipase C, and V_2 receptors to adenylate cyclase, which is activated by occupied receptor. AVP is a more potent agonist for both V_1 and V_2 receptors than oxytocin. These receptors are seven-transmembrane-domain proteins characteristic of G-protein-coupled receptors. Examples, from *Rattus norvegicus*, V_{1a} receptor: database code V1AR_RAT, 395 amino acids (44.48 kDa); V_{1b} receptor: database code V1BR_RAT, 425 amino acids (47.08 kDa); V_2 receptor: database code V2R_RAT, 371 amino acids (40.75 kDa). *See also* **oxytocin receptor**.

vasostatin a 76 amino-acid peptide released by proteolytic cleavage of **chromogranin** A; it lowers vascular tension.

vasotocin a vasoactive peptide, closely related in amino-acid sequence to arginine **vasopressin** and **oxytocin**, that is secreted by the posterior pituitary gland in birds, reptiles, and some amphibians. It has the sequence

Cys-Tyr-Ile-Gln-Asn-Cys-Pro-Arg-Gly-amide,

with a disulfide bond between the two cysteines.

VASP *abbr. for* vasodilator-stimulated phosphoprotein; a substrate for cyclic AMP- and cyclic GMP-dependent protein kinases in platelets. It is associated with actin filaments and focal adhesions and is a proline-rich **profilin** ligand. Example from *Canis familiaris*: database code VASP_CANFA, 384 amino acids (40.41 kDa).

VCAM *abbr. for* vascular cell adhesion molecule; a class of **adhesion molecules** belonging to the immunoglobulin superfamily. The class is exemplified by VCAM-1 (CD106; molecular mass 90–110 kDa). This is expressed on endothelial cells, macrophages, dendritic cells, fibroblasts, and myoblasts, and is inducible within 6–10 h by interleukin 1β, interleukin 4,

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tumour necrosis factor α, or interferon γ. It binds to VLA-4 (*see* **VLA**) and integrin $\alpha_4\beta_7$ (*see* **integrin**), and mediates adhesion of lymphocytes, monocytes, and eosinophils to activated endothelium. Example from human: database code VCA1_HUMAN, 739 amino acids (81.28 kDa). Residues 1–24 are the signal, 25–698 the extracellular domain, with seven Ig-like C_2 domains.

vector **1** *or* **vector quantity** a quantity specified by its direction and sense as well as by its magnitude. **2** *(in pathology)* an organism that carries an organism of a different species from one place to another, especially one that transfers a **pathogen** between hosts, either mechanically (**mechanical vector**) or by playing a specific role in the pathogen's life cycle (**biological vector**). *Compare* **vehicle** (def. 2). **3** *(in genetics) see* **cloning vector**.

vectorette a synthetic DNA oligonucleotide with a mismatched region. Vectorettes are ligated to genomic fragments and serve in a variety of **polymerase chain reaction** (PCR) systems in which the sequence of only one primer is available.

vectorial enzyme any enzyme, such as one fixed in a membrane, that is directional in its action, e.g. **sodium/potassium ATPase**.

vectorial processing processing of a fully formed precursor polypeptide into a mature protein when used to drive the movement of the protein from one aqueous compartment (e.g. the cytoplasm) through a membrane into a second aqueous compartment (e.g. an intramitochondrial or intrachloroplastal space). *Compare* **vectorial translation**.

vectorial translation the stage of **translation** in the biosynthesis of any protein destined for export from a cell, where a nascent polypeptide being produced on a **polysome** bound to the membrane of the rough endoplasmic reticulum in a eukaryote is conducted through the membrane by its N-terminal **signal peptide**. *Compare* **vectorial processing**.

vegetal hemisphere glycoprotein 1 *abbr.*: Vg-1; a glycoprotein, belonging to the TGF-β family (*see* **transforming growth factor**), that serves to facilitate the differentiation of either mesoderm or endoderm, either as a cofactor in an instructive signal or by providing a permissive environment. Example from *Xenopus*: database code DVR1_XENLA, 360 amino acids (41.72 kDa).

vegetal pole the end at which most of the yolk is located e.g. in an amphibian egg; the end opposite the **animal pole**.

vegetative describing cells or tissues that are engaged in nutrition and growth rather than sexual reproduction, and excluding dormant forms.

vegetative bacteriophage the intrabacterial genome of a **bacteriophage** when it is noninfective but is controlling the synthesis by the host of components necessary for the production of new, infective bacteriophage particles.

vegetative reproduction **1** *(in plants)* a form of **asexual reproduction** in which new individuals develop from specialized multicellular organs (e.g. bulbs, corms, tubers) that break off from the parent plant. **2** *(sometimes)* a term used to describe **budding** (def. 2) and similar forms of asexual reproduction in animals such as coelenterates and sponges.

VEGF *abbr. for* vascular endothelial growth factor.

vehicle **1** any inert medium with which a biologically active substance (e.g. a drug) is mixed or in which it is dissolved, suspended, or emulsified in order to increase its bulk and/or to facilitate its absorption after administration. **2** any agent (animate or inanimate) of transmission, especially of infection; *see also* **vector** (def. 2).

vein **1** *(in animals)* the blood vessels conducting blood from the tissues. **2** *(in plants)* a vascular bundle in a leaf.

velocity of reaction *an alternative name for* **rate of reaction**.

venom any toxic animal secretion that is produced by discrete glands and is delivered by a specific mechanism for defensive or offensive purposes.

venombin either of two serine proteinases found in snake venom. **Venombin AB** EC 3.4.21.55; *other name*: gabonase (from the venom of the gaboon viper, *Bitis gabonica*); it cleaves Arg-|-Xaa bonds in fibrinogen to form fibrin and release fibrinopeptides A and B; it is not inhibited by antithrombin III or hirudin. **Venombin A** EC 3.4.21.74; it cleaves Arg-|-Xaa bonds in fibrinogen to form fibrin and release fibrinopeptide A, but further reaction depends on species; it is a trypsin-like enzyme; example: precursor (zymogen) from *Bothrops atrox* (fer-de-lance): database code BATX_BOTAT, 255 amino acids (28.16 kDa); six putative S–S bonds and two glycosylation sites.

venous of, or relating to, a **vein**, or to the blood in the veins.

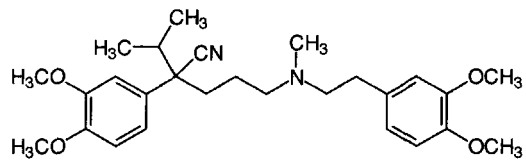
ventilation the passage of air into and out of the respiratory tract, or other confined space.

Ventolin *see* **salbutamol**.

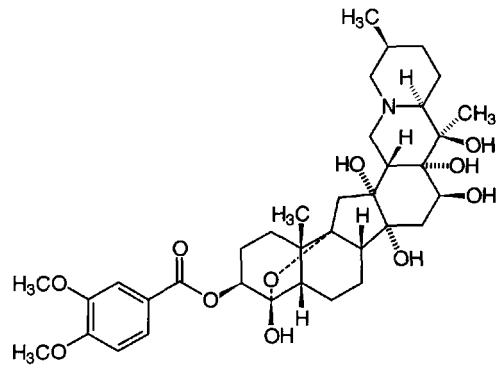
Vent polymerase *or (sometimes)* **Deep Vent polymerase** *the proprietary name for* thermostable DNA polymerases used as alternatives to ***Taq* DNA polymerase** in the **polymerase chain reaction**. These enzymes provide a higher fidelity than the *Taq* DNA polymerase, derived in part from their exonuclease activity. They derive from the archaeon *Thermococcus litoralis*, isolated from a submarine thermal vent, hence the enzyme's name.

ventral situated towards the belly surface of an animal.

verapamil α-3-{[2-(3,4-dimethoxyphenyl)ethyl]methylamino}propyl-3,4-dimethoxy-α-(1-methylethyl)benzeneacetonitrile; iproveratril; D365; a Ca^{2+}-blocking agent used clinically in the treatment of cardiac disorders and in the laboratory to inhibit the movement of calcium ions across biological membranes. Its action is similar to that of **nifedipine**. Nifedipine binds to the dihydropyridine binding site of vascular voltage-operated **calcium channels**, but verapamil probably acts at another related site. *See also* **D600**.



veratridine a toxic alkaloid, $C_{36}H_{51}NO_{11}$, found in the seeds of a plant, *Schoenocaulon officinalis*, of the lily family; it also occurs in the rhizome of *Veratrum album*. It blocks the development of the action potential involved in axonal conduction, binding to the Na^+ channels and blocking them in the open configuration.



v-erbA related protein *see* **COUP**

verbascose the tetrasaccharide, *O*-α-D-galactopyranosyl-(1→6)-*O*-α-D-galactopyranosyl-(1→6)-*O*-α-D-glucopyranosyl-

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(1→2)-β-D-fructofuranoside. It occurs in roots of the mullein, *Verbascum thapsus*.

verdoperoxidase *see* **myeloperoxidase**.

verification **1** establishment of the correctness of a theory, fact, etc. **2** a term used to describe the deacylation of misacylated tRNA molecules by the specific aminoacyl-tRNA synthase.

Verner–Morrison syndrome *or* **pancreatic cholera** *or* **WDHA syndrome** a disease syndrome of humans characterized by the following features, the first three of which are obligatory: tumour, severe watery diarrhoea, achlorhydria or hypochlorhydria, weight loss, and dehydration. The tumours (**VIPomas**) are mostly of pancreatic origin (some are neurogenic) and produce **vasoactive intestinal polypeptide** (VIP), the circulating levels of which are raised. [After John Victor Verner (1927–), US physician and Ashton Byrom Morrison (1922–), US pathologist.]

Veronal *a proprietary name for* **barbital**.

Versene *a proprietary name for* the tetrasodium salt of **edetate**.

versican *or* **large fibroblast proteoglycan** *or* **chondroitin sulfate proteoglycan core protein 2** a protein that plays a role in intercellular signalling. The N-terminal part is similar to a glial hyaluronate-binding protein; in the middle of the protein there are glucosaminoglucan attachment sites; the C-terminal part contains EGF-like repeats (*see* **epidermal growth factor**) and a lectin-like domain. Example (precursor) from human: database code PGCS_HUMAN, 2409 amino acids (264.76 kDa).

vertical rotor a rotor for use in an **ultracentrifuge**. The wells holding the tubes are drilled parallel to the axis of rotation and at right angles to the lines of the centrifugal force.

very-low-density lipoprotein *abbr.*: VLDL; one of the classes of lipoproteins found in blood plasma in many animals (data normally relate to humans). VLDL is also known as pre-β-lipoprotein because its electrophoretic mobility is slightly greater than that of low-density, or β-lipoprotein. VLDL particles have diameter 25–70 nm, solvent density for isolation (g mL^{-1}) <1.006, hydrated density (g mL^{-1}) 0.97. Their approximate composition (% by weight) is 5–8% unesterified cholesterol, 11–14% esterified cholesterol, 20–23% phospholipid, 44–60% triacylglycerol, 4–11% protein. Their apolipoprotein composition (% by weight total apolipoprotein) is 36.9% B-100, 49.9% C-I + C-II + C-III, 13% E-II + E-III + E-IV. They are synthesized in liver and are the precursor of low-density lipoprotein.

very-low-density-lipoprotein receptor *abbr.*: VLDL receptor; a membrane protein that binds VLDL, accumulates in clathrin-coated pits, and internalizes VLDL. It has a large extracellular domain, a single transmembrane domain, and a small intracellular domain. Example from human: database code LDVR_HUMAN, 873 amino acids (96.09 kDa); residues 1–27 are the signal, 28–797 the extracellular domain, and 820–873 the cytoplasmic domain.

vesicle a closed structure, found only in eukaryotic cells, that is completely surrounded by a unit membrane but, unlike a **vacuole**, contains material that is not (or is not known to be) in the liquid state.

Vg-1 *abbr. for* vegetal hemisphere glycoprotein 1.

VHDL *abbr. for* very-high-density lipoprotein.

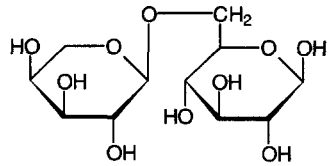
viability a measure of the capacity of a cell for metabolism and division. It is often estimated experimentally by determining the number of cells that exclude normally membrane-impermeant dyes, e.g. **Trypan Blue**.

Viagra *a proprietary name for* sildenafil; 5-[2-ethoxy-5-(4-methylpiperazin-1-yl)phenyl]-1-methyl-3-propyl-1,6-dihydro-7*H*-pyrazolo[4,3-d]pyrimidin-7-one; used clinically for the oral treatment of male erectile dysfunction. It selectively and potently inhibits a specific phosphodiesterase that hydrolyses cyclic GMP; this second messenger mediates the action of nitric oxide in normal erectile function, an action which is thus potentiated.

VIC *abbr. for* vasoactive intestinal contractor; *see* **endothelin**.

vic- *prefix (in chemical nomenclature)* denoting the presence of **vicinal** (def. 2) substituents.

vicianose the disaccharide 6-*O*-α-L-arabinosyl-D-glucose, obtained from a glycoside in seeds of *Vicia angustifolia*.



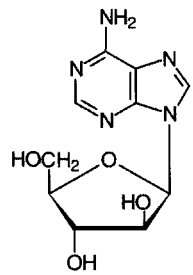
β-D-anomer

vicillinpeptidohydrolase *see* **legumain**.

vicinal **1** adjacent, neighbouring. **2** *(in organic chemistry)* describing two (usually identical) atoms or groups attached one to each of two linked carbon atoms in a molecular structure. The presence of vicinal substituents is denoted by the prefix *vic-* attached to the name of the compound. *Compare* **geminal**.

vicilin a major storage protein in seeds of *Pisum sativum* (pea); it comprises 124 amino acids, M_r 170 000. Legumin-like and vicilin-like globulins are the main storage proteins of most angiosperms and gymnosperms.

vidarabine adenine arabinoside; 9-β-D-arabinofuranosyladenine; a purine nucleoside, a metabolite of hypoxanthine arabinoside, produced by *Streptomyces antibioticus*. Its triphosphate derivative inhibits viral DNA polymerase and may be incorporated into viral DNA; it also inhibits DNA synthesis.



vigabatrin γ-vinyl-γ-aminobutyric acid; γ-vinyl GABA; 4-amino-5-hexenoic acid; an irreversible inhibitor of the enzyme GABA transaminase (**4-aminobutyrate transaminase**), which metabolizes the neurotransmitter γ-amino-*n*-butyric acid.

Vigneaud *see* **du Vigneaud**.

villin a Ca^{2+}-regulated actin-binding protein occurring in the microvilli of intestinal epithelial cells and kidney proximal tubule cells. Villin consists of a large core fragment, the N-terminal portion, and a small headpiece, the C-terminal portion; the headpiece binds F-actin (*see* **actin**) strongly in both the presence and absence of Ca^{2+}; it is similar to **gelsolin**. Example from human: database code VIL1_HUMAN, 826 amino acids (92.46 kDa).

vimentin a protein found in class III **intermediate filaments** in mesenchymal and other nonepithelial cells and in the Z disk of skeletal and cardiac muscle cells. It is a phosphoprotein, phosphorylation being enhanced during cell division. Example from human: database code VIME_HUMAN, 465 amino acids (53.49 kDa).

vinblastine a structurally complex alkaloid, $C_{46}H_{58}N_4O_9$, obtained from *Vinca rosea*, that binds to spindle microtubules and arrests metaphase of mitosis. It is used as an antineoplastic agent.

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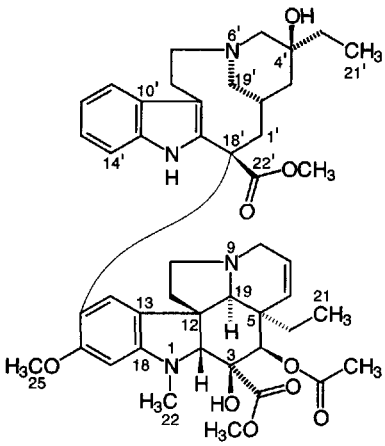
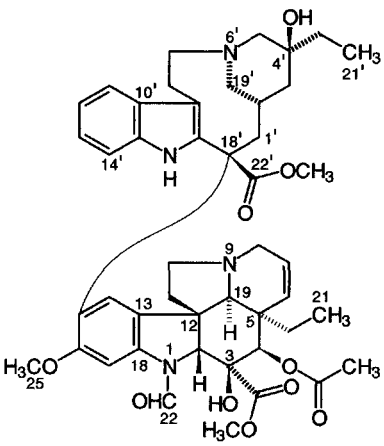


vinblastine

vincristine an alkaloid, $C_{46}H_{56}N_4O_{10}$, obtained from *Vinca rosea* and with a structural relationship to **vinblastine**, that binds to spindle microtubules and arrests metaphase of mitosis. It is used as an antineoplastic agent.



vinculin a cytoskeletal protein associated with the cytoplasmic face of the focal adhesion plaques that anchor actin microfilaments to the plasma membrane and that attach a cell to the substratum. It associates with **talin** in binding **integrins** to the cytoskeleton. Vinculin is phosphorylated (on serines, threonines, and tyrosines) and acylated by myristic acid and/or palmitic acid. Vinculin and metavinculin are produced by alternative splicing of the same gene. Metavinculin differs from vinculin in having a 68-residue additional domain near the C terminus. Example from human: database code VINC_HUMAN, 1065 amino acids (116.46 kDa).

vindoline the major alkaloid from *Vinca rosea*; $C_{25}H_{32}N_2O_6$. It is without physiological activity but constitutes a pentacyclic moiety of **vinblastine** and **vincristine**.

vinyl ether alk-1-enyl ether; a class of compounds characterized by a bond formed between a long-chain aldehyde and one (in the case of monoalk-1-enyl ethers) or two (for dialk-1-enyl ethers) of the hydroxy groups of the glycerol moiety of a glycerolipid; only the *sn*-1 isomers occur naturally, and chains of 16 or 18 carbons are usual. Such glycerophospholipids are known as **plasmalogens**; ethanolamine glycerophospholipids characteristically contain larger amounts of plasmalogens than other classes, and heart tissue is rich in plasmalogens.

γ-vinyl GABA *see* **vigabatrin**.

viosamine 4-amino-4,6-dideoxy-D-glucose; a component of the lipopolysaccharide of some strains of *Escherichia coli*.

VIP *abbr. for* vasoactive intestinal polypeptide.

VIPoma a tumour producing **vasoactive intestinal polypeptide** (VIP). It is often associated with a watery diarrhoea and other pathological signs known as **Verner–Morrison syndrome**.

viral particle *see* **virion**.

viral RNA RNA that constitutes the genome of certain viruses – the RNA viruses. Examples are poliovirus, which has single-stranded RNA, and cytoplasmic polyhedrosis virus of the tussock moth, which has 10 double-stranded RNA molecules. All **retroviruses** contain RNA as the genome.

virino a name coined for a putative novel type of particulate, noncellular, submicroscopic, transmissible, pathogenic agent, as typified by the agent responsible for **scrapie**. The infective particle was believed to consist of a small nucleic-acid molecule covered with host-specified protein. *See* **prion**.

virion *or* **viral particle** the complete particle of a virus, found extracellularly and capable of surviving in crystalline form and of infecting a living cell. It comprises the nucleic-acid **core** and the protein **capsid**; the latter may be enclosed by an **envelope** in some viral families.

virogene *see* **oncogene hypothesis**.

viroid any member of a group of about 30 autonomously replicating plant pathogens. They consist of single-stranded circular RNA of about 350 nucleotides containing much self-complementarity. They have no genes, so do not express protein. It is assumed that the viroid RNA acts as its own template, subverting host cell enzymes to carry out the replication. The product consists of concatamers of daughter strands that undergo self-cleavage to form new viroid RNA genomes. It is likely that hammerhead structures (*see* **ribozyme**) are involved. An example is potato spindle tuber viroid (PSTV). This is similar to human hepatitis delta which is part viroid and part virus in that the mechanism of replication is like that of a viroid and part of the genome is homologous with PSTV.

virology the scientific study of viruses and the diseases caused by them. —**virological** *adj.*; **virologist** *n.*

viropexis the process by which virus particles are adsorbed onto the surface of a cell and then taken into the cytoplasm.

Virtanen, Artturi Ilmari (1895–1973), Finnish agricultural chemist; Nobel Laureate in Chemistry (1945) 'for his research and inventions in agricultural and nutrition chemistry, especially for his fodder preservation method'.

virulence the capacity of a microorganism or virus to cause disease in a host under certain conditions. —**virulent** *adj.*

virulent phage a bacteriophage that invariably lyses the bacterium it infects. Virulent phages have no alternative but to follow the **lytic cyle**.

virus a noncellular infective agent that is capable of reproducing only in an appropriate host cell. Viruses are typically smaller than bacteria, and can infect animal, plant, or bacterial cells (*see* **bacteriophage**); many are important agents of disease. The infective particle (**virion**) consists of a core of nucleic acid (either DNA or RNA) surrounded by a proteinaceous **capsid** and, in some cases, an outer envelope. A virus can interact with its host cell in several different ways. In a lytic interaction the cell's replicative and protein biosynthetic apparatus is directed by the viral genes to produce numerous progeny virions, which are released upon disintegration of the host cell (*see* **lytic cycle**). However, in a persistent infection, low levels of virus production may be sustained without destruction of the host cell. In a **latent infection**, the virus resides in a host cell without undergoing replication, although it may be provoked to enter the lytic phase by some stimulus. Oncogenic viruses, which include both DNA viruses and RNA viruses

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(**retroviruses**) carry **oncogenes** and are potentially capable of transforming their host cells into tumour cells. Animal viruses have been divided into seven classes according to the nature of their genome and the mechanism of synthesis of messenger RNA (*see* **Baltimore classification**).

virusoids *see* **satellite RNA**.

visceral layer *see* **serous membrane**.

viscometer *or* **viscosimeter** an apparatus for measuring the viscosity or resistance to flow of a liquid.

viscosity *symbol*: η; the resistance to flow of a fluid due to the sum of the effects of adhesion and cohesion. Consider a liquid between two parallel plates, one of which is moving in the x direction with a velocity v. The liquid is thought of as a number of layers, each of which slides along the adjacent layer; the frictional resistance between adjacent layers generates a velocity gradient in the y direction. The deformation of the liquid produced by the velocity gradient is known as **shear** (def. 1). The frictional force, f, between the liquid layers is proportional to the area, A, of the layers and to the velocity gradient between them, such that $f = \eta A(\mathrm{d}v/\mathrm{d}y)$, where η is the **coefficient of viscosity** or simply the viscosity; $f/A = F$, the **shear stress**; and $\mathrm{d}v/\mathrm{d}y = G$, the **shear gradient** or **shear rate**. If η is independent of F or G, the fluid is a **Newtonian fluid**; if η is a function of F or G, the fluid is a **non-Newtonian fluid**.

visinin a calcium-binding protein specific to cone photoreceptors; a chicken isoform with homology to bovine **recoverin** has three Ca^{2+}-binding sites. Example from *Gallus gallus*: database code VISI_CHICK, 191 amino acids (22.39 kDa).

visual cascade the sequence of reactions occurring after the absorption of a photon by a **rhodopsin** molecule. It eventually leads to a rapid fall in cyclic GMP levels, which closes Na^+ channels in the membrane of the visual receptor and activates the nerve impulse in the optic nerve. The activated rhodopsin stimulates the G-protein **transducin** which initiates the signal-transduction cascade.

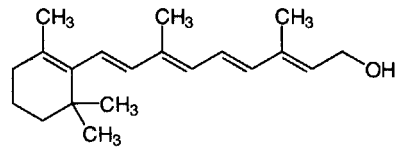
visual purple *see* **rhodopsin**.

vitalism a doctrine stating that that the phenomena of biology are due to a vital principle distinct from physicochemical forces, and cannot be explained by the laws of physics and chemistry alone. The accidental discovery, in 1890, by the brothers Büchner that a cell-free extract of yeast could catalyse alcoholic fermentation did much to convince any lingering adherents that such a doctrine was untenable. Also important was Wohler's synthesis of urea (a natural product) from ammonium cyanate in 1828.

vitamer any of two or more chemically and metabolically related compounds that display qualitatively the same biological activity as a vitamin. For example, retinol, retinal, retinoic acid, 3,4-didehydroretinol, and various carotenes are all vitamers of vitamin A.

vitamin an organic substance that is distributed in foodstuffs (and sometimes in intestinal bacteria) in relatively minute amounts, is distinct from the main organic components of food (i.e. protein, carbohydrate, and fat), and is needed for the normal nutrition of the organism (or species) in question. Deficiency or absence of any particular vitamin causes a corresponding specific deficiency disease. **Vitamins A**, **D**, **E**, and **K** are the fat-soluble vitamins; **vitamins B_1**, **B_2**, **B_6**, **B_{12}**, and **C**, plus **biotin**, **choline**, **folic acid**, **nicotinic acid**, and panthothenic acid (*see* **pantothenate**), are the water-soluble vitamins.

vitamin A **1** *a common name for* **retinol**. **2** *a generic name for* any retinoid exhibiting qualitatively the biological activity of retinol. Included, in addition to retinol (relative activity 100) are: **retinal** (91); **retinoic acid** (≈65); **3,4-didehydroretinol** (40); **3,4-didehydroretinal**; and **3,4-didehydroretinoic acid** (the activities relative to retinol being measured by the standardized growth test on vitamin A-deficient rats). Vitamin A is fat-soluble, and is present in various lipid-containing animal preparations, especially liver and dairy products. Vitamin A activity is displayed also by various carotenes; these act as provitamins, which are converted to retinal in the small intestine in most vertebrates. The vitamin A of commerce was originally a preparation of, or extract from, fish-liver oils, which contain large amounts of retinol, principally as its palmitate; it is now largely derived chemically. Proper vitamin A nutrition is necessary for: (1) somatic function, including growth and differentiation, e.g. of epithelial structures and bone; (2) reproduction, including spermatogenesis, oogenesis, placental development, and embryonic growth; and (3) visual processes (*see* **retinal**, **3,4-didehydroretinal**). Vitamin A deficiency signs include stunted growth, thickening of various membranes by keratinization, and, in the eye, night blindness, xerophthalmia, keratomalacia, and eventually complete blindness. In moderate excess, vitamin A is highly toxic.



vitamin A_1 *an alternative name (not recommended) for* **retinol**.

vitamin A_2 *an alternative name (not recommended) for* **3,4-didehydroretinol**.

vitamin A acid *or* **vitamin A_1 acid** *an alternative name (not recommended) for* **retinoic acid**.

vitamin A_2 acid *an alternative name (not recommended) for* **3,4-didehydroretinoic acid**.

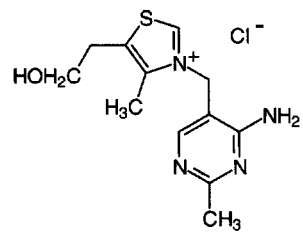
vitamin A alcohol *or* **vitamin A_1 alcohol** *an alternative name (not recommended) for* **retinol**.

vitamin A_2 alcohol *an alternative name (not recommended) for* **3,4-didehydroretinol**.

vitamin A aldehyde *or* **vitamin A_1 aldehyde** *an alternative name for (not recommended)* **retinal**.

vitamin A_2 aldehyde *an alternative name (not recommended) for* **3,4-didehydroretinal**.

vitamin B_1 *or* **thiamine** *or (sometimes)* **thiamin** *or (formerly)* **aneurin(e)** 3-(4-amino-2-methylpyrimidin-5-ylmethyl)-5-(2-hydroxyethyl)-4-methylthiazolium chloride; a water-soluble vitamin, present in fresh vegetables and meats, especially liver. Deficiency in humans causes beriberi, signs of which include cardiopathy and neuropathy; in pigeons, a characteristic head-drop is an overt sign of deficiency. Its diphosphoric ester, **thiamine diphosphate** (*abbr.*: TPP), formerly known as **cocarboxylase**, is a coenzyme for oxidative decarboxylation and other enzymic reactions, including ones catalysed by pyruvate and oxo-glutarate dehydrogenases, pyruvate decarboxylase, and transketolase.



vitamin B_2 *or* **riboflavin** 6,7-dimethyl-9-ribitylisoalloxazine; *formerly also called* lactoflavin, hepatoflavin, ovoflavin, uroflavin, vitamin G, vitamin H. A water-soluble vitamin, present in most foods but especially in milk and meat products. It is a component of the **flavin nucleotide** coenzymes (e.g. FAD, FMN). Isolated from milk and eggs by Kuhn and co-

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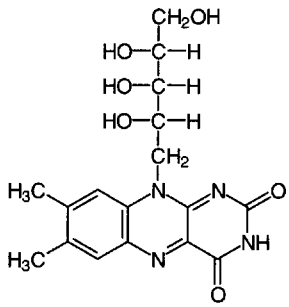
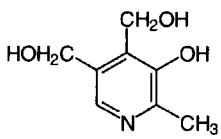
workers in 1933 and chemically synthesized by them and others in 1935. Significant deficiency seldom occurs, but can cause inflammation of the tongue and lips and sores in the corners of the mouth.

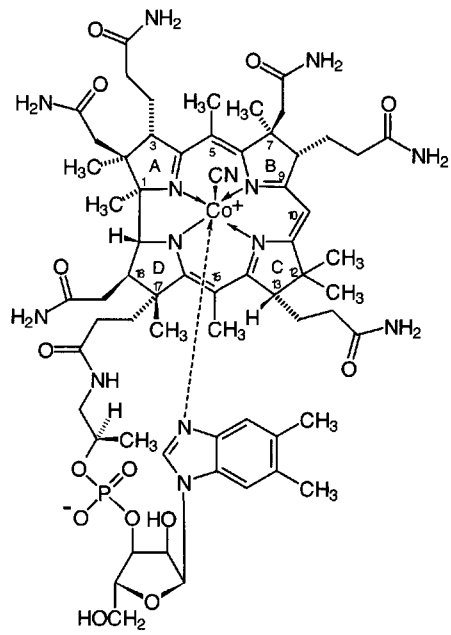


vitamin B_5 *(rarely) an alternative name for* pantothenic acid; *see* **pantothenate**.

vitamin B_6 *or* **pyridoxine** 2-methyl-3-hydroxy-4,5-bis(hydroxymethyl)pyridine; a water-soluble vitamin; **pyridoxal** and pyridoxamine also act as vitamers. It is present in many foods, including meats (largely as pyridoxal or pyridoxamine), and plant sources (largely as pyridoxine) such as cereals, lentils, nuts, and vegetables. Pyridoxal phosphate is a coenzyme for many enzyme reactions including those involving transamination, amino-acid decarboxylation, racemization, and modifications to amino-acid side chains. Deficiency is not a major problem and signs are difficult to produce.



vitamin B_{12} *or* **cobalamin** *or* **cobamide** a water-soluble vitamin, of which there are several structurally related forms. All are characterized by possession of a **corrin** nucleus containing a cobalt atom. Four of the cobalt coordinate bonds are liganded by nitrogens of the four pyrrole rings found in the corrin nucleus; the fifth position is occupied by the ribonucleotide of 5,6-dimethylbenzimidazole, which is also linked via a 1-amino-2-propanol moiety to one of the pyrrole rings; the sixth position is variously occupied by a cyanide group (cyanocobalamin, the form in which the molecule was first isolated, the cyanide group having been introduced during extraction), or a methyl group (**methylcobalamin**, one of the forms in which the molecule acts as a coenzyme), or a 5′-deoxyadenosyl group (**deoxyadenosylcobalamin**, the other active coenzyme form). Vitamin B_{12} is present only in foods of animal origin, especially liver, fish, and eggs. The coenzyme forms are needed for two classes of enzyme: members of the first class, exemplified by **methylmalonyl-CoA mutase**, require the deoxyadenosyl form; members of the second, exemplified by 5-methyltetrahydrofolate-homocysteine *S*-methyltransferase, (EC 2.1.1.13) require the methyl form (*see* **5-methyltetrahydrofolate**). In normal individuals, deficiency rarely occurs, but is precipitated by lack of **intrinsic factor**, a protein secreted by gastric mucosa and required for efficient absorption of the vitamin. Lack of intrinsic factor leads to **pernicious anemia**, investigation of which first led to the discovery of cobalamin.



cyanocobalamin

vitamin B_{12r} reductase *see* **cob(II)alamin reductase**.

vitamin C ascorbic acid; a water-soluble vitamin, and the first vitamin to be recognized. Awareness of the ability of fresh vegetables and fruit to prevent **scurvy** is attributed to the British physician James Lind (1716–94), who published *A Treatise on Scurvy* in 1757. The active compound was first isolated by A. **Szent-Györgyi** in 1928 as 'hexuronic acid', a strong reducing substance from rat adrenals and citrus fruits. This was shown four years later to be identical with the anti-scorbutic substance isolated by Zilva and associates. Vitamin C is widely distributed in vegetables and fruit, but easily destroyed by cooking. *See* **ascorbic acid** for structure. *See also* **L-gulonolactone oxidase**.

vitamin D *the common and class name for* any steroid that exhibits qualitatively the biological activity of calciol (= vitamin D_3 – *see below*); the antirachitic vitamin. All such compounds are fat-soluble substances structurally related to either the parent hydrocarbon, **cholestane**, or its 24-methyl derivative, ergostane, and all are 9,10-seco-sterols, i.e. 3-hydroxysteroids in which bond breakage has occurred between C-9 and C-10 in ring B of the steroid nucleus. Separately numbered variants of vitamin D, with their recommended trivial names in parentheses, are: **vitamin D_2** *or* calciferol (**ercalciol** *or* **ergocalciferol**), the variant formed in plants by the action of UV light on the endogenous provitamin **ergosterol** and produced industrially by UV-irradiation of ergosterol isolated from yeast; **vitamin D_3** (**calciol** *or* **cholecaliferol**), the variant occurring naturally in particularly high concentrations in the liver oils of certain fish, especially cod, halibut, or tunny, and produced non-enzymically in the skin of animals by the action of a UV component (230–313 nm) of sunlight on the provitamin 7-dehydrocholesterol; **vitamin D_4** (22,23-dihydroercalciol *or* (24*S*)-methylcalciol or *(formerly)* 22,23-dihydroergocalciferol), the variant produced by irradiation of 22,23-dihydroergosterol; **vitamin D_5** ((24*S*)-ethylcalciol); and **vitamin D_6** ((22*E*)-(24*R*)-ethyl-22,23-didehydrocalciol). (**Vitamin D_1**, a designation now obsolete, was found to be a mixture of ercalciol and lumisterol.) Of these variants, calciol (D_3) and ercal-

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ciol (D_2) are the most significant. In addition, vitamin D activity is displayed by several unnumbered synthetic derivatives or isomers of calciol (or of ercalciol) and by the 25-hydroxylated and 1α,25-dihydroxylated metabolites **calcidiol** and **calcitriol** (or **ercalcidiol** and **ercalcitriol**). Calcidiol (or ercalcidiol) is formed in liver from calciol (or ercalciol) and converted in kidney to calcitriol (or ercalcitriol), the physiologically active form of vitamin D_3 (or D_2). Vitamin D mediates the absorption of calcium and phosphate ions from the intestine and promotes the mineralization of bone. The vitamin D deficiency conditions of **rickets** (in children) and **osteomalacia** (in adults) may be treated by administration of the vitamin, commonly as D_2. Overdosage of vitamin D results in disturbances of calcium metabolism and ultimately leads to decalcification of bone. *See also* **calcitetrol**. For structures see entries for individual compounds.

vitamin D binding protein *abbr.*: DBP; a multifunctional protein found in plasma, ascitic fluid, cerebrospinal fluid, and urine, and on the surface of many cell types. In plasma it carries the vitamin D sterols; it also prevents polymerization of actin by binding its monomers. DBP associates with membrane-bound immunoglobulin on the surface of B lymphocytes, and with IgG Fc receptor on the membranes of T lymphocytes. Example (precursor) from human: database code VTDB_HUMAN, 474 amino acids (52.90 kDa).

vitamin E α-tocopherol; a fat-soluble vitamin considered to act primarily as an antioxidant. Other tocopherols (*see* **tocopherol** for structure) have vitamin E activity. Vitamin E is thought to prevent the formation of lipid autoxidation products, an action resulting from its ability to trap free radicals and thus to prevent the chain reaction leading to further peroxide formation. It is present in vegetable-seed oils, and also in meat, milk, and eggs. Deficiency occurs in practice only in pathological states in which absorption is affected, and can result in premature red cell death. A relative deficiency may occur when the intake of polyunsaturated fatty acids is high unless the diet is supplemented with α-tocopherol.

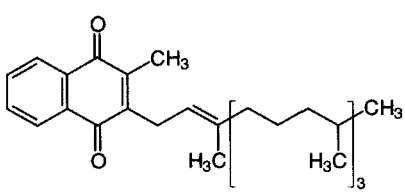
vitamin F *(formerly) a collective term for* **essential fatty acids**.

vitamin G *an old name for* riboflavin (i.e. **vitamin B_2**).

vitamin H **1** *(sometimes) an alternative name for* **biotin**. **2** *an old name for* riboflavin (i.e. **vitamin B_2**).

vitamin H_1 *(sometimes) an alternative name for* ***p*-aminobenzoic acid**.

vitamin K 2-methyl-3-phytyl-1,4-naphthoquinone; phylloquinone; 3-phytylmenadione; vitamin K_1; a fat-soluble vitamin required for the synthesis of prothrombin and certain other **blood coagulation** factors. The **menaquinones** (vitamins K_2) are also active. Vitamin K is found in green leafy vegetables, meat, and milk. Deficiency is uncommon because it is produced by gut bacteria, but gut sterilization may trigger symptoms (decrease in plasma prothrombin) if intake is defective. Vitamin K acts as a cofactor in the post-translational formation of 4-carboxyglutamyl residues in certain proteins, e.g. **blood coagulation** factors VII. IX. X, and especially prothrombin, during which an epoxidase reaction occurs to convert vitamin K_1 to its epoxide form, which is converted back by a reductase. This reductase can be inhibited by **warfarin**, which thus reduces vitamin K_1 levels, thereby reducing prothrombin formation and so acting as an anticoagulant.



vitamin-K-epoxide reductase (warfarin-sensitive) EC 1.1.4.1; an enzyme that catalyses the formation of 2-methyl-3-phytyl-1,4-naphthoquinone, oxidized dithiothreitol, and H_2O from 3-epoxy-2,3-dihydro-2-methyl-3-phytyl-1,4-naphthoquinone and 1,4-dithiothreitol.

vitellogenin the precursor protein of **lipovitellin** and **phosphitin**, a major egg-yolk protein synthesized in the liver of chickens and *Xenopus*. It has an M_r of 135 000 and is split in the ovary into its constituent proteins. In *Xenopus*, two genes, for vitellogenin I and II, are spread over more than 21 kbp of DNA, their primary transcripts consisting of 6 kbp of **pre-mRNA** with 33 **introns**. Example from *Gallus gallus* (precursor): database code VIT2_CHICK, 1850 amino acids (204.81 kDa). A related protein is found in *Drosophila melanogaster*. Example (precursor) from *D. melanogaster*: database code VIT1_DROME, 439 amino acids (48.66 kDa).

vitronectin *or* **serum spreading factor** an adhesion protein, present in plasma and on the external surface of membranes of tissues, that promotes the adhesion of cells in tissue culture. The $\alpha_v\beta_3$ **integrin** binds vitronectin, fibrinogen, laminin, von Willebrand factor, fibronectin, and thrombospondin. Example from human (precursor): database code VTNC_HUMAN, 478 amino acids (54.31 kDa). Residues 1–19 are the signal, 20–478 vitronectin; residues 20–63 are somatomedin B (*see* **somatomedin**).

VI *symbol for* the valeryl group.

VLA a family of **integrins** all having the β_1 subunit. They comprise VLA-1, $\alpha_1\beta_1$ (β subunit also called VLAβ, glycoprotein IIa or gpIIa, CD29; α subunit also called CD49a), which binds laminin (and collagen); VLA-2, $\alpha_2\beta_1$ (α subunit also called gpIa, CD49b), which binds collagen (and laminin); VLA-3, $\alpha_3\beta_1$ (α subunit also called CD49c), which binds fibronectin, laminin, and collagen; VLA-4, $\alpha_4\beta_1$ (α subunit also called CD49d), which binds VCAM-1 and fibronectin; VLA-5 (*or* fibronectin receptor), $\alpha_5\beta_1$ (CD49e), which binds fibronectin; VLA-6 (*or* laminin receptor), $\alpha_6\beta_1$ (CD49f), which binds laminin; $\alpha_7\beta_1$, which binds laminin; $\alpha_8\beta_1$, ligand doubtful; and $\alpha_v\beta_1$ (α subunit also called vitronectin receptor subunit, CD51), which binds fibronectin.

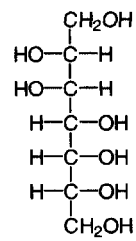
VLDL *abbr. for* very-low-density lipoprotein.

VMA *abbr. for* vanillylmandelic acid; *see* **hydroxymethoxymandelate**.

VMS an **operating system** implemented on DEC VAX computers.

void volume **1** *(in column chromatography)* the volume of the mobile phase, i.e. total **bed volume** of the column minus the volume occupied by the support particles. **2** *(in gel chromatography) or (sometimes)* **exclusion volume** the volume of the mobile phase passing through the gel required to elute a molecule that never entered the stationary phase.

volemitol D-*glycero*-D-*talo*-heptitol; a substance widely distributed in plants, fungi, and lichens. It is used as a sweetening agent.



volkensin a ricin-like toxic glycoprotein, purified from the roots of *Adenia volkensii*, a Kenyan shrub. It consists of two subunits, A (M_r 29 000) and B (M_r 36 000), linked by disulfide bonds.

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volt *symbol*: V; the SI derived unit of electric potential or electromotive force. It is equal to the difference in electric potential between two points on a conductor carrying a constant current of one ampere when the power dissipated between the points is one watt. 1 V = 1 W A^{-1} = 1 J C^{-1}. [After Alessandro Volta (1745–1827), Italian physicist.]

voltage-gated ion channel a channel in a cell membrane whose opening is governed by the membrane potential.

voltameter *an old term for* **coulometer**.

voltametry *an old term for* **coulometry**.

voltammetry an electroanalytical procedure for identifying and determining the concentrations of various ions in solution by studying the relation between a varied electric potential applied between two electrodes immersed in a test solution and the resultant faradaic current. It includes **anodic stripping voltammetry** and **polarography**. —**voltammetric** *adj.*; **voltammetrically** *adv.*

volume of distribution *symbol*: V_d; the theoretical volume of fluid in which a specified dose of drug is distributed, based on measurement of the concentration of free drug (i.e. that not bound to plasma proteins) in plasma. $V_d = Q/C_p$, where Q is the amount of drug administered and C_p is the concentration in plasma.

volutin granule *or* **metachromatic granule** an electron-dense cytoplasmic inclusion found in various bacteria, yeasts, and other microorganisms. It exhibits **metachromasia** on staining with certain basic dyes, contains polymetaphosphate, and is believed to serve as a phosphate store. *See also* **Babes–Ernst body**.

von Euler **1 Hans von Euler**, *see* **Euler** (def. 1). **2 Ulf Svante von Euler** (1905–83), son of H. von Euler (*see* **Euler** (def. 1)), Swedish neurophysiologist and pharmacologist notable for his recognition of the importance of norepinephrine as the main neurotransmitter in mammalian adrenergic neurons; Nobel Laureate in Physiology or Medicine (1970) jointly with J. Axelrod and B. Katz 'for their discoveries concerning the humoral transmittors in the nerve terminals and the mechanism of their storage, release and inactivation'.

von Gierke's disease *see* **glycogen disease**.

von Hevesy *see* **Hevesy**.

von Laue *see* **Laue**.

von Willebrand factor *abbr.*: vWFa; a blood protein involved in blood clotting. It performs two important hemostatic functions: it links specific platelet membrane receptors to collagen and possibly other components of subendothelial connective tissue, so mediating platelet adhesion to sites of vascular damage, and it binds to and stabilizes factor VIII (*see* **blood coagulation**). Deficiency results in bleeding from skin due to failure of platelet adhesion, with a prolonged bleeding time, and also results in spontaneous bleeding into joints and soft tissues due to the secondary factor VIII deficiency caused by the instability of factor VIII. The primary translation product, synthesized by vascular endothelial cells and megakaryocytes, is a protein of 2813 amino acids (309.29 kDa): database code VWF_HUMAN. Residues 1–22 are a signal peptide, 23–763 a peptide that is cleaved off and is known as **von Willebrand antigen II**, and the mature protein, residues 764–2813. Cysteine is the most abundant amino acid. Before the mature factor is secreted from cells of origin, many intermolecular disulfide bridges between vWF molecules are formed that lead to a complex that may vary in mass from dimers of about 500 kDa to species of more than 20 megadaltons. Inherited defects of vWF affect nearly 1% of the population, but most are not clinically significant. The majority of patients have a quantitative deficiency of vWF, with autosomal dominant inheritance and are known as type I. Type II variants have an abnormal vWF. In vWF deficiency (*abbr.*: vWD) type IIA intermediate and large complexes are absent. Mutations cluster near Tyr^{842}-|-Met^{843}, a site that is sensitive to proteolysis. vWD type III is rare, and is a severe autosomal recessive disease characterized by virtual absence of vWF, in some cases known to be due to total or partial deletion of the vWF gene. Unactivated platelets bind vWF through gpIb–IX complex, deficiency of which leads to a bleeding disorder, **Bernard-Soulier syndrome**. After activation, platelets bind vWF through the **integrin** gpIIb–IIIa complex, which is defective in **Glanzmann thrombasthenia**, another bleeding disorder. [After Erik Adolph von Willebrand (1870–1949), Finnish physician.]

V8 proteinase *see* **glutamyl endopeptidase**.

vps34 *or* **vacuolar sorting protein 34** a protein trafficking protein that is involved in the sorting and segregation of vacuoles. It is a homologue of **1-phosphatidylinositol 3-kinase**, having that enzymic activity, which may be the mechanism by which it acts. It is in turn activated by phosphorylation by a serine/threonine protein kinase, vps15. Example from *Saccharomyces cerevisiae*: database code VP34_YEAST, 875 amino acids (100.92 kDa).

VRE *abbr. for* **vancomycin**-resistant *Enterococcus* (erstwhile *Streptococcus*). It is one of a number of drug-resistant pathogens (*compare* **MRSA**) found in hospital populations of bacteria. The resistance is due to an enzymic modification of the peptidoglycan precursor that is the target for vancomycin.

v-*yes* *see* ***YES***.

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Ww

w *symbol for* **1** mass fraction. **2** work (alternative to *W*). **3** speed (alternative to *u*, *v*, or *c*). **4** (bold italic) velocity (alternative to *v*, *u*, or *c*).

W *symbol for* **1** watt. **2** a residue of the α-amino acid L-tryptophan (alternative to Trp). **3** a residue of an incompletely specified base in a nucleic-acid sequence that may be adenine or may be thymine (in DNA) or uracil (in RNA). **4** a residue of the minor nucleoside **wyosine** (alternative to Y). **5** tungsten.

W *symbol for* **1** weight (alternative to *G* or *P*). **2** work (alternative to *w*). **3** radiant energy (alternative to *Q*). **4** writhing number.

W3 *one abbr. for* **World Wide Web**.

Waksman, Selman Abraham (1888–1973), Russian-born US soil microbiologist; Nobel Laureate in Physiology or Medicine (1952) 'for his discovery of streptomycin, the first antibiotic effective against tuberculosis'. *See also* **Schatz**.

Wald, George (1906–97) US physiologist; Nobel Laureate in Physiology or Medicine (1967) jointly with R. Granit and H. K. Hartline 'for their discoveries concerning the primary physiological and chemical visual processes in the eye'.

Walden inversion the inversion of the configuration at a chiral centre in a bimolecular nucleophilic substitution reaction. [After its discoverer, Paul Walden (1863–1957), Latvian chemist.]

Waldenström's macroglobulinemia a lymphoid tumour that arises from the most mature B lymphocytes and invariably produces IgM, which appear as a **paraprotein**. [After Jan Goesta Waldenström (1906–), Swedish physician.]

wall effect **1** *(in centrifugation)* the collision of sedimenting molecules with the wall of the cell. This occurs because the centrifugal field is radial, so can be avoided by using sector-shaped cells. **2** *(in chromatography)* the curving and spreading of a zone as it migrates down a chromatographic column because of inhomogeneities in solvent flow near the wall of the column.

Warburg, Otto Heinrich (1883–1970), German physiologist and biochemist; Nobel Laureate in Physiology or Medicine (1931) 'for his discovery of the nature and mode of action of the respiratory enzyme'.

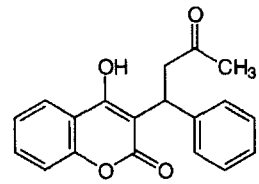
Warburg apparatus a sensitive, constant-volume respirometer for measuring gas exchange of cells, homogenates, or tissue slices. It consists of a small flask, with one or more side arms for the addition of reagents, and a centre well, connected to a U-tube manometer of about 1 mm^2 internal cross-section, fitted with a reservoir for manometer fluid. The vessel is immersed in a constant temperature bath and shaken continually to equilibrate the gas in the liquid phase, where the reaction is taking place, with the gas in the gas phase, where the reaction is being measured. It was used extensively for metabolic studies before the wide availabilty of radioactive tracers, but is now virtually obsolete.

Warburg–Dickens–Horecker pathway *or* **Warburg–Dickens pathway** *an alternative name for* **hexose monophosphate pathway**.

Warburg effect **1** the relative overproduction of lactate that occurs in many tumours. **2** the inhibitory effect of high oxygen concentrations on photosynthesis.

Warburg's enzyme *an alternative name for* old yellow enzyme; *see* **yellow enzyme**.

warfarin 3-(α-phenyl-β-acetylethyl)-4-hydroxycoumarin; 1-(4′-hydroxy-3′-coumarin-3′-yl)-1-phenylbutan-3-one; an anticoagulant and rodenticide. Its action derives from its ability to inhibit the reductase that converts the epoxide form of **vitamin K** to its reduced form, which is a cofactor for the production of the 4-carboxyglutamyl residues essential for the activity of, among other proteins, the **blood coagulation** factors II (i.e. prothrombin), VII, IX, and X. [From the name of the patentees, Wisconsin Alumni Research Foundation, + coumarin.] *See also* **vitamin-K-epoxide reductase (warfarin-sensitive)**.



Waring blendor *the proprietary name for* a blender used in the preparation of tissue homogenates. It consists of a hydrodynamically designed vessel (of tetrafoil cross-section) in the bottom of which a specially shaped blade rotates at high speed. [After the manufacturers, Waring Products Corporation.]

washing soda *see* **soda**.

Wasserman reaction a form of **complement-fixation test** for human blood and cerebrospinal fluid, widely used in the past to detect syphilitic infection, although false positive reactions were often given by yaws, leprosy, paroxysmal hemoglobinuria, and even malarial infection. The antigen on which the test was based proved to be **cardiolipin**. [After August von Wassermann (1866–1925), German bacteriologist.]

water balance (of an organism) the **water intake** (as a liquid, the water in food, and water of oxidation) less the **water output** (water in urine, feces, or other excreta, water expended in saturating respired air, water lost through the integument).

waterfall sequence *an alternative name for* **cascade sequence**.

water regain (of an ion-exchange resin) for cationic resins, the weight of water taken up by 1 g dry resin in the hydrogen form; for anionic resins, the weight of water taken up by 1 g dry resin in the chloride form.

water-soluble B *an old name for* a fraction rich in water-soluble vitamins prepared from egg yolk.

Watson, James Dewey (1928–), US biologist; Nobel Laureate in Physiology or Medicine (1962) jointly with F. H. C. Crick and M. H. F. Wilkins 'for their discoveries concerning the molecular structure of nuclear [*sic*] acids and its significance for information transfer in living material'. *See also* **Franklin**.

Watson–Crick model of DNA a model that envisages one form of **DNA** (deoxyribonucleic acid) as consisting essentially of two antiparallel helical polynucleotide chains coiled around the same axis to form a double helix. The deoxyribose–phosphate backbones lie on the outside of the helix and the purine and pyrimidine bases lie approximately at right angles to the axis on the inside of the helix. The diameter of the helix is 2.0 nm and there is a residue on each chain every 0.34 nm in the *z* direction. The angle between each residue on the same chain is 36°, so that the structure repeats after 10 residues (3.4 nm) on each chain. The two chains are held together by hydrogen bonds between pairs of bases, each member of the pair belonging to a different polynucleotide chain. Adenine is always paired with thymine and guanine with cytosine. The two chains are therefore complementary. Watson and Crick's paper, published in *Nature* in 1953, also contained a prescient statement: 'It has not escaped our notice that the specific pairing we have postulated immediately suggests a possible copying mechanism for the genetic material.' The structure of DNA proposed by Watson and Crick has stood the test of time. It is difficult to exaggerate the importance of the short paper. To quote from L. Stryer's *Biochemistry* (fourth edi-

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tion), 'This brilliant accomplishment ranks as one of the most significant in the history of biology because it led the way to an understanding of gene function in molecular terms.' *See also* **double helix**. [After J. D. **Watson** and F. H. C. **Crick**.]

watt *symbol*: W; the SI derived unit of power or radiant flux; it is the power dissipated when one joule is expended in one second; i.e. 1 W = 1 J s^{-1}. [After James Watt (1736–1819), British engineer.]

wave function *symbol*: ψ *or* Ψ *or* Φ *or* ϕ; the amplitude of the wave associated with a particle, e.g. an electron, as obtained from the Schrödinger wave equation. The square of the value of ψ at any point is proportional to the probability of finding the particle at that point.

wavelength *symbol*: λ; the distance between successive points of equal phase of a wave. Wavelength is equal to the velocity of the wave motion divided by its frequency. For electromagnetic radiation, $\lambda = c_0/\nu$, where c_0 is the velocity of light *in vacuo* and ν the frequency of the radiation.

wavenumber *or* **repetency** for an electromagnetic radiation (e.g. light), the reciprocal of the **wavelength**; i.e. the number of waves in unit distance. *Compare* **kayser**.

wax **1** any lipid fraction from living organisms or from crude petroleum that is a plastic substance, hard when cold, easily moulded when warm, and insoluble in water. **2** any fatty-acid ester of a long-chain monohydroxy alcohol.

wax synthase *see* **long-chain-alcohol *O*-fatty-acyltransferase**.

Wb *symbol for* weber.

WBC *or* **wbc** *or* **w.b.c.** *abbr. for* white blood cell(s); *see* **leukocyte**.

WDHA syndrome *abbr. for* watery diarrhoea, hypokalemia, plus achlorhydria syndrome; i.e. **Verner–Morrison syndrome**.

weak interactions noncovalent interactions between molecules and parts of molecules, including charge–charge interactions, those involving permanent dipoles, van der Waals forces, and hydrogen bonds. They are particularly important in protein and nucleic-acid structure.

weber *symbol*: Wb; the SI derived unit of magnetic flux. It is equal to the flux that, linking a circuit of one turn, produces in it an emf of one volt as it is reduced to zero at a uniform rate in one second; i.e. 1 Wb = 1 V s. [After Wilhelm Eduard Weber (1804–91), German physicist.]

wee1 a gene in *Schizosaccharomyces pombe* encoding a protein kinase (EC 2.7.1.112) that can phosphorylate tyrosine and serine/threonine residues. In yeast it phosphorylates a single tyrosine of cdc2; in the human it phosphorylates both a tyrosine and a threonine of the equivalent protein. It has conserved catalytic domains of the other (serine/threonine) type of protein kinase. The protein acts as a negative regulator for entry to mitosis; it closely resembles the corresponding human protein kinase. Example from *S. pombe*: database code WEE1_SCHPO, 877 amino acids (96.26 kDa). *See also* ***cdc* gene**.

weight average molecular mass *old name for* mass average molar mass; *see* **average molar mass**.

Weigle reactivation *see* **W reactivation**.

Wernicke–Korsakoff syndrome a combination of **Wernicke's disease** (gliosis and capillary proliferation leading to ocular manifestations and polyneuropathy) and **Korsakoff's psychosis** (difficulty in recording and retaining new impressions). Wernicke's disease is due to vitamin B_1 deficiency, and manifests particularly in patients with a genetic abnormality in transketolase resulting in its reduced affinity for thiamine diphosphate. In such patients, even mild B_1 deficiency, as often occurs in alcoholics, may produce symptoms. [After Karl Wernicke (1848–1905), German alienist, and Sergei Sergeyevich Korsakoff (1854–1900), Russian neurologist.]

Western blotting a technique for **blotting** proteins onto nitrocellulose, nylon, or other **transfer membrane** after they have been resolved by gel electrophoresis. The proteins can then be detected by one of several methods, including autoradiography (if labelled), or through binding to fluorescently labelled, ^{125}I-labelled, or enzyme-linked (*see* **ELISA**) antibody, lectin, or other specific binding agent. The name derives by extension through the cardinal points from **Southern blotting**, the first such blotting technique, with a capital initial by similar extension.

Whitaker plot a plot that, ideally, gives a linear correlation between the logarithm of the relative molecular mass of a macromolecule and the ratio of the **elution volume**, V, to the **void volume**, V_o, when the macromolecules in solution are passed through a suitable **gel filtration** column; i.e. log $M_r = V/V_o$. [After John Robert Whitaker (1929–), US biochemist.]

white adipose tissue *or* **white fat** a highly specialized tissue developed particularly in mammals and birds to store fat to supply energy to the whole animal. The cells contain a single large droplet of fat that, in the nourished state, fills most of the cell. The nucleus is somewhat flattened and is in the narrow band of cytoplasm around the cell's periphery. Adipose tissue is found in many parts of the body but tends to be concentrated under the skin (subcutaneous) and around internal organs (heart and kidney). The stored fat consists principally of triacylglycerols. *Compare* **brown adipose tissue**.

white blood cell *see* **leukocyte**.

white fat *see* **white adipose tissue**.

white muscle pale, skeletal, usually involuntary muscle that is relatively deficient in myoglobin and cytochromes. *Compare* **red muscle**.

Wieland, Heinrich Otto (1877–1957), German chemist; Nobel Laureate in Chemistry (1927) 'for his investigations of the constitution of the bile acids and related substances'.

wild-type the **phenotype** that is characteristic of most of the members of a species occurring naturally and contrasting with the phenotype of a **mutant**. *Compare* **auxotroph**.

Wilkins, Maurice Hugh Frederick (1916–), New Zealand-born British biophysicist; Nobel Laureate in Physiology or Medicine (1962) jointly with F. H. C. Crick and J. D. Watson 'for their discoveries concerning the molecular structure of nuclear [*sic*] acids and its significance for information transfer in living material'. *See also* **Franklin**.

Wilkinson, (Sir) Geoffrey (1921–96), British inorganic chemist noted for his extensive studies of transition-metal complexes with organic compounds and for the discovery of rhodium complexes now used as catalysts in industrial hydrogenation reactions; Nobel Laureate in Chemistry (1973), the prize being shared with E. O. Fischer 'for their pioneering work, performed independently, on the chemistry of the organometallic, so called sandwich compounds'.

Willstätter, Richard Martin (1872–1942), German organic chemist; Nobel Laureate in Chemistry (1915) 'for his researches on plant pigments, especially chlorophyll'.

Wilm's tumour *or* **nephroblastoma** a malignancy in human infants (incidence 1 in 10 000) associated with protein **WT33**. [After Marx Wilms (1867–1918), German pathologist.]

Wilson, Charles Thomson Rees (1869–1959), British physicist; Nobel Laureate in Physics (1927) 'for his method of making the paths of electrically charged particles visible by condensation of vapour' [prize shared with A. H. Compton].

Wilson's disease *or* **hepatolenticular degeneration** a rare autosomal recessively inherited disease characterized by degenerative changes in the brain, particularly in the basal ganglia, and cirrhosis of the liver. There are excessive deposits of copper in the liver, brain, cornea, and kidney; the serum copper is usually low and there is a **ceruloplasmin** deficiency. Patients may be effectively treated with British antilewisite (**dimercaprol**) or other chelating agents. [After (Samuel Alexander) Kinnier Wilson (1878–1937), US-born British neurologist.]

Wilzbach method a method for the random labelling of a compound with tritium by exposing it to isotopically pure tritium gas in a sealed container for several weeks. The exchange is promoted by the radiation.

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Windaus, Adolf Otto Reinhold (1876–1959), German chemist; Nobel Laureate in Chemistry (1928) 'for the services rendered through his research into the constitution of the sterols and their connection with the vitamins'.

winding angle (of a DNA double helix) the angle of rotation between successive base pairs.

winding number the number of double-helical turns in a closed-circular DNA measured relative to a surface on which the DNA helix lies. *See also* **supercoil**.

windowless counter a counter for radioactive (or X-ray) ionization in which the sample (or source) is not separated from the detector by a membrane or 'window'.

wingless a gene in *Drosophila melanogaster* that codes for a protein in the **WNT family**, probably a growth factor that acts on neighbouring cells to regulate the ***engrailed*** gene. Database code WNTG_DROME, 468 amino acids (51.93 kDa). A gene for a homologous protein is present in the brachiopod *Terebratulina retusa*.

WNT family a protein family that includes several proteins (e.g. WNT-2 from human and mouse) that are probably signalling molecules in tissue development. They are encoded by *WNT* genes. The *WNT-1* gene is closely homologous to ***wingless***. Example, WNT-2 (precursor) from human: database code WNT2_HUMAN, 360 amino acids (40.37 kDa).

wobble base the third base in the anticodon of **transfer RNA** (5′ end). It can bind to one of several possible bases at the 3′ end of the codon in mRNA. *See also* **wobble hypothesis**.

wobble hypothesis a hypothesis that in **translation** during protein synthesis a less strict specificity in the base pairing of the 5′ base of the anticodon of **transfer RNA** (tRNA) allows it to make alternative hydrogen-bonding with the third base of the codon of messenger RNA (mRNA) beyond the usual G–C and A–U pairings. Specifically, anticodon U may recognize A or G and anticodon G may recognize C or U; then A no longer has a unique meaning at this position, since the U that recognizes it also recognizes G; the same applies to the codon U, which can also be recognized by G. In practice, although the hypothesis has been fully supported by experiment, UGG and AUG are the only examples of the first type of wobble, and no examples of the second type are known. The presence of bases other than U, A, G, or C at the anticodon 5′ position also contributes to more general pairing at this position than would be the case if G–C, A–U specificity were strictly observed. Thus, bases such as **wyosine**, **queuosine**, and **inosine** may be present (I always substitutes for A) with less strict pairing constraints. The degeneracy at the third codon position is consistent with the fact that about 40 different tRNA molecules interact with the 61 possible sense codons. Not all of the different tRNA structures have been determined, so it is not possible to state with certainty the structure of all the anticodons, although possible structures can be predicted. In the case of $tRNA^{Ala}$ the structure of the two tRNAs is known.

Wolfgram proteolipid protein one of the three principal classes of central nervous system **myelin protein**, extractable by chloroform:methanol (2:1, v/v) and consisting of three main fractions of 235, 54, and 62 kDa. *Compare* **Folch–Lees protein**. [After F. Wolfgram, who first discovered it.]

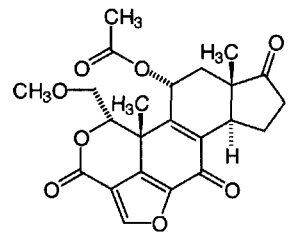
Wood, Harland Goff (1907–91), US biochemist distinguished particularly for work on fixation of CO_2; the reaction between pyruvate and CO_2 became known eponymously as the **Wood–Werkman reaction**. For 46 years he worked in the Department of Biochemistry at Case Western Reserve University. Described by Hanson as an 'American original' born and raised in the American heartland.

Woodward, Robert Burns (1917–79), US organic chemist; Nobel Laureate in Chemistry (1965) 'for his outstanding achievements in the art of organic synthesis'.

work *symbol*: *W or w*; the transfer of energy expressed as the product of a force, *F*, and the distance, *s*, through which its point of application moves in the direction of the force; i.e. $W = \int F\,ds$. The SI unit of work is the joule. The manifestation of work in productive form usually involves transduction by a mechanical device of the action of a force through a distance. A relationship between the work done on (or by) a system of constant mass, the heat it gains (or loses), and the change in the internal energy of the system is provided by the first law of thermodynamics (*see* **thermodynamics**).

World Wide Web *abbr.*: WWW; *or* **W3**; an **Internet** facility for viewing and recovering archival material including an extensive range of biochemical and molecular biological data. Examples are included in **Appendix B** and **Appendix C**. *See also* **Appendix D**.

wortmannin *or* **MS-54** *or* **KY 12420** a potent inhibitor of smooth muscle myosin light chain kinase and protein kinase C produced by the fungal strain *Talaromyces wortmanni* KY12420. It is also a potent selective, cell-permeable and irreversible inhibitor of **1-phosphatidylinositol 3-kinase**.



W reactivation *or* **Weigle reactivation** *or (formerly)* **UV reactivation** the phenomenon whereby the survival of UV-irradiated bacteriophage is higher in a UV-irradiated host than in an unirradiated host. [After Jean Jacques Weigle (1901–68), who discovered it and described it in 1953.]

writhing number *symbol*: W; an index of the superhelical coiling of DNA, termed **writhe**. The writhing number and the **twist number** between them determine the **linking number** (L). The writhing number does not have a precise quantitative definition, but represents the degree of supercoiling. A decrease in L involves some decrease in supercoiling, and an increase in L an increase in supercoiling. *See also* **supercoil**.

wt *or* **wt.** *abbr. for* weight.

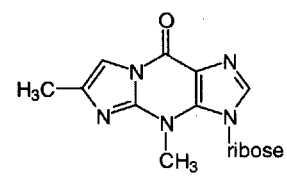
WT33 a protein that is related to **early growth response proteins** and is associated with **Wilm's tumour**; it is probably a tumour suppressor. Other mutations are associated with Denys–Drash syndrome. It has alternative splice sites, a zinc finger, and four motifs. Example from human: database code WT1_HUMAN, 449 amino acids (49.13 kDa).

w/v *or* **wt/vol.** *abbr. for* weight per unit volume (of a solution or mixture).

w/w *or* **wt/wt** *abbr. for* weight per unit weight (of a solution or mixture).

WWW *abbr. for* **World Wide Web**.

wyosine *symbol*: W *or* Y; any of a number of modified forms of guanosine present in the anticodon loop of some species of **transfer RNA**. All are based on the structure N^2-(2-methyletheno)guanosine, and carry varying side chains on the five-carbon imidazo ring. The structure of one such compound is shown. *See also* **minor nucleoside**.



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Xx

x *symbol for* **1** amount-of-substance fraction (i.e. mole fraction) or number fraction for condensed phases. *Compare* ***y***. **2** a Cartesian space coordinate, complementary to *y* and *z*.

X **1** *symbol for* **a** a residue of an unknown, unspecified, or (specified) unusual α-amino acid (alternative to Xaa). **b** a residue of the ribonucleoside **xanthosine** (alternative to Xao). **2** *abbr. for* X Windows.

X *symbol for* (electric) reactance.

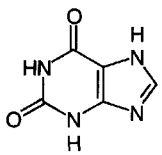
X-537A *an alternative name for* **lasaloacid**.

Xaa *symbol for* a residue of an unknown, unspecified, or (specified) unusual α-amino acid (alternative to X).

Xan *symbol for* a residue of the purine base **xanthine**.

xanthan gum a capsular complex heteropolysaccharide formed by strains of the pseudomonad bacterium *Xanthomonas campestris* and believed to promote adhesion of the organism to its plant host. It is widely used in the cosmetic, food, and other industries as a crystallization inhibitor, emulsifier, gelling agent, etc.

xanthine *symbol*: Xan; 2,6-dihydroxypurine; 2,6-dioxopurine; 3,7-dihydro-1*H*-purine-2,6-dione; a purine formed in the metabolic breakdown of guanine but not present in nucleic acids. *Compare* **hypoxanthine**. *See also* **allopurinol**.



xanthine oxidase EC 1.1.3.22; *the recommended name for* hypoxanthine oxidase; *systematic name:* xanthine:oxygen oxidoreductase; a flavoprotein (FAD) enzyme containing iron and molybdenum, abundant in milk and liver, that catalyses the oxidation of **xanthine** to urate and superoxide (or hydrogen peroxide) and also the oxidation of hypoxanthine to xanthine. It was formerly known as **Shardinger enzyme**. The enzyme can exist in two forms. One, known as xanthine dehydrogenase, has **NAD** as coenzyme, and urate and NADH as products. The other form, xanthine oxidase, reacts with dioxygen and has urate and H_2O_2 as products. The dehydrogenase is converted reversibly to the oxidase by oxidation of sulfhydryl groups or irreversibly by proteolysis. Example from *Rattus norvegicus*: database code XDH_RAT, 1330 amino acids (146.11 kDa). Example from human (homodimer): database code XDH_HUMAN, 1338 amino acids (147.76 kDa).

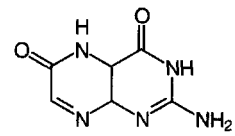
xanthinuria the excretion of excessive amounts of xanthine in the urine. It is sometimes due to a hereditary disease in which there is a gross deficiency of **xanthine oxidase** activity in the tissues.

xantho+ *or (before a vowel)* **xanth+** *comb. form* denoting yellow.

xanthophyll any **carotenoid** in which one or more oxygenated functions are present in the molecule.

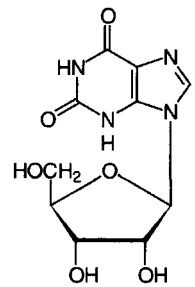
xanthoproteic test a qualitative test for protein in which a yellow colour (or precipitate from solution) is formed on addition of conc. nitric acid; the yellow colour turns orange when made alkaline.

xanthopterin a yellow pterin pigment of insect wings, e.g. of the common sulfur butterfly. *Compare* **leukopterin**.



xanthopterin

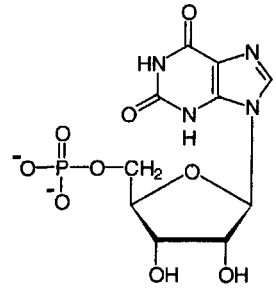
xanthosine *symbol*: X *or* Xao; xanthine riboside; 9-β-D-ribofuranosylxanthine; a nucleoside formed by the deamination of guanosine.



xanthosine monophosphate *abbr.*: XMP; *an alternative name for* any xanthosine phosphate, but in particular for xanthosine 5′-phosphate, especially when its distinction from xanthosine (5′-)diphosphate and xanthosine (5′-)triphosphate requires emphasis.

xanthosine phosphate xanthosine monophosphate (*abbr.*: XMP); any phosphoric monoester or diester of xanthosine. Of the three possible monoesters – the 2′-phosphate, the 3′-phosphate, and the 5′-phosphate – and the two possible diesters – the 2′,3′-phosphate and the 3′,5′-phosphate – only **xanthosine 5′-phosphate** is known to occur naturally (the locant being omitted if no ambiguity may arise).

xanthosine 5′-phosphate *or* **5′-xanthylic acid** *or* **5′-phosphoxanthosine** *or* **5′-*O*-phosphonoxanthosine** *symbol*: Xao5′*P*; *alternative recommended names for* xanthosine monophosphate (*abbr.*: XMP); xanthosine 5′-(dihydrogen phosphate); xanthine (mono)ribonucleotide. (The locant is commonly omitted if there is no ambiguity as to the position of phosphorylation.) It is an intermediate in the biosynthesis of guanosine 5′-phosphate, 5′-guanylic acid, GMP. XMP is formed from inosine 5′-phosphate, 5′-inosinic acid, by an NAD^+-dependent dehydrogenase on the pathway for synthesis of guanine nucleotides; a glutamine-requiring amidotransferase reaction (catalysed by **GMP synthase**) then converts XMP to GMP.



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xanthylic acid *the trivial name for* any phosphoric monoester of xanthosine. The position of the phosphoric residue on the ribose moiety of a given ester may be specified by a prefixed locant (*see* **xanthosine phosphate**). However, 5′-xanthylic acid is the ester commonly denoted, its locant usually being omitted if no ambiguity may arise. 5′-Xanthylic acid is also an alternative recommended name for **xanthosine 5′-phosphate**.

Xao *symbol for* a residue of the ribonucleoside **xanthosine** (alternative to X).

Xao5′*P* *symbol for* xanthosine 5′-phosphate.

Xao5′*PP* *symbol for* xanthosine 5′-diphosphate (alternative to ppX).

Xao5′*PPP* *symbol for* xanthosine 5′-triphosphate (alternative to pppX).

X cell *see* **X-Y-Z cell theory**.

X chromosome a **sex chromosome**. It is often found paired in the **homogametic** sex, which in many species is the female, and single in the **heterogametic** sex, in many species the male. The X chromosome carries a large number of genes which control many aspects of development and function. A mutant gene which is so carried is called X linked. Since males possess only one X chromosome an abnormal gene that it carries cannot be paired with a normal allele; the male is then said to be hemizygous for that particular mutant gene. The female in whom both members of a pair of X-linked genes are identical is said to be homozygous for that gene; if the members of a gene pair are dissimilar the woman is called a heterozygote or carrier for the abnormal allele. One X chromosome is inactivated during early embryonic development so that individuals do not have a double dose of genes on the X chromosome. Since the descendants of each cell retain the same inactivated X chromosome, a proportion of cells have the paternal X chromosome in an inactive state while in the other cells the maternal X chromosome is active. Hence the female who is heterozygous for an abnormal gene will have two types of cells, one with the normal and one with the mutant gene. She is said to be a mosaic. *Compare* **Y chromosome**. *See also* **sex determination**.

X-chromosome inactivation inactivation in females of one of the two **X chromosomes** during early embryonic development; this phenomenon occurs randomly in all cells of the embryo. Thus, the cells in a female are mosaic in respect to which of the X chromosomes is functional – that from the father or the mother. *See also* **X chromosome**.

XDP *abbr. for* xanthosine (5′-)diphosphate.

Xe *symbol for* xenon.

xenin a 25-residue peptide isolated from human gastric mucosa. The six C-terminal amino acids are identical to those of the octapeptide, **xenopsin**, present in the skin of amphibians. It stimulates exocrine pancreatic secretion, rising in plasma after a meal. Example from human: database code XENI_HUMAN, 25 amino acids (2.97 kDa).

xenite a subsidiary organism in a **synxenic** culture.

xeno+ *or (before a vowel)* **xen+** *comb. form* indicating something strange or foreign.

xenobiochemistry the biochemistry of organic compounds foreign to the organism.

xenobiotic **1** any substance that does not occur naturally but interacts with the metabolism of any organism. **2** of, or relating to, substances that are foreign to living systems.

xenobiotic-response element *abbr.*: XRE; a DNA-regulatory sequence that binds transcription factors responsible for activation of gene expression for enzymes that detoxify a number of xenobiotics, including halogenated and other aryl hydrocarbons. *See also* ***Ah***.

xenogeneic *or* **xenogenic** originating in a different species, especially of a tissue transplant. *See also* **xenograft**.

xenograft a tissue graft between individuals of different species.

Xenopus laevis the South African clawed toad, the oocytes and embryos of which have been extensively exploited in molecular genetics and vertebrate embryology. The large oocytes were used for pioneering studies of the microinjection of nucleic acids directly into the nucleus, a technique now extended to other species.

xenotope an antigenic **epitope** that is foreign to a particular animal.

xenotype a class or group of related **xenotopes**; *i.e.* an antigenic **epitype** that is foreign to a particular animal.

xeroderma pigmentosum an autosomal recessive hereditary skin disease of humans in which homozygotes show a marked tendency to develop skin cancers following exposure to sunlight. It is due to a reduced ability to excise UV-induced cyclobutane **pyrimidine dimers** from DNA.

xerophthalmia a condition in which there is progressive drying and wrinkling of the conjunctiva of the eye. One cause is **vitamin A** deficiency.

X-gal *abbr. for* 5-bromo-4-chloro-3-indolyl-β-D-galactoside, a colourless substrate that is hydrolysed by β-galactosidase to a blue product. It is used with **cloning vectors** containing part of the *lacZ* gene to select recombinants in molecular cloning: the peptide produced by the *lacZ* fragment complements the defective β-galactosidase enzyme in host cells. Insertion of foreign DNA into the vector inactivates the *lacZ* gene, so host cells containing recombinant plasmids will grow as white colonies on medium containing X-gal, whereas host cells containing 'empty' vectors will have a functional β-galactosidase and thus produce blue colonies.

xi *symbol*: ξ (lower case) *or* Ξ (upper case); the fourteenth letter of the Greek alphabet. For uses *see* **Appendix A**.

Xiphophorus a genus of fish, that includes the South American minnow, some species of which have been much used for the study of inherited characteristics involved in carcinogenesis. Crossing of certain species, e.g. backcrossing *X. maculatus* (platyfish) with *X. helleri* (swordtail: recurrent parent) leads to spontaneous development of melanoma.

Xis protein *or* **excisionase** the product of the *xis* gene in lambda phage: database code VXIS_LAMBD, 72 amino acids (8.60 kDa). It plays an essential role in the excision step of release of phage DNA from **prophage**. *See also* **integrase**.

XMP *abbr. for* xanthosine monophosphate; i.e. xanthosine (5′-)phosphate.

xotch a transmembrane protein in *Xenopus* that is similar in sequence, and presumably in role, to the product of ***notch***. It is uniformly expressed in early embryos. It contains 36 EGF-like domains and three notch-type repeats. Example from *Xenopus laevis*: database code NOTC_XENLA, 2524 amino acids (275.12 kDa).

X-Pro dipeptidase EC 3.4.13.9; *other names*: proline dipeptidase; imidodipeptidase; prolidase; peptidase D; γ-peptidase; an enzyme that catalyses the hydrolysis of Xaa-|-Pro dipeptides; it also acts on aminoacyl-hydroxyproline analogues, but has no action on Pro-|-Pro. It requires manganese. Example from human: database code PEPD_HUMAN, 492 amino acids (54.19 kDa).

XPS *abbr. for* X-ray photoelectron spectroscopy; *see* **photoelectron spectroscopy**.

X-ray crystallography the study of the geometric forms of crystals by **X-ray diffraction**. Myoglobin was the first protein for which the structure was solved by X-ray crystallography.

X-ray diffraction a method that uses the diffraction pattern obtained by passing X-rays through crystals, or other regular molecular arrays, to measure interatomic distances and to determine the three-dimensional arrangement of atoms (or molecules) in the structure studied. For the pattern to be sharp, the wavelength of the radiation used must be shorter than the regular spacing between the elements of the structure. X-rays typically have wavelengths of only a few tenths of a nanometre, making them suitable for biological samples. X-ray diffraction is used extensively in the determination of structures of proteins and nucleic acids and many other natural products (an early landmark was, together with chemical evidence, the determination of the structure of penicillin). In order to re-

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solve the phase differences, much use has been made of **isomorphous replacement** with heavy metal atoms in these structural studies.

X-ray photoelectron spectroscopy *abbr.*: XPS; *see* **photoelectron spectroscopy**.

X-rays *or (sometimes, esp. US)* **x-rays** *or (formerly)* **röntgen rays** electromagnetic radiation emitted by atoms during extranuclear loss of energy of incident radiation (e.g. high-energy electrons, gamma radiation) or by atoms of certain radionuclides during transformation by **electron capture**. X-rays have wavelengths in the range 1 pm–10 nm (frequencies 3 PHz–3 EHz). This range lies above that of gamma radiation and overlaps the wavelengths of the far ultraviolet. Characteristic X-rays have specific wavelengths of a particular nuclide or target element. *See also* **bremsstrahlung**, **synchrotron**.

XRE *abbr. for* xenobiotic-response element.

XTP *abbr. for* xanthosine (5′-)triphosphate.

Xul *symbol for* a residue (or sometimes a molecule) of the ketopentose xylulose.

X Windows a graphical interface, often simply called X, for UNIX and VMS computers. Many molecular graphical and other programs (including **ACeDB**) use X.

xyl+ *a variant (sometimes before a vowel)* of **xylo+**.

Xyl *symbol for* a residue (or sometimes a molecule) of the aldopentose xylose.

xylan any of a group of homopolysaccharides of **xylose**, consisting mainly of β-1,4-linked xylopyranose units with various substituent groups, that occur in the cell walls of higher plants, and in some marine algae. Xylans form the major glycans of the **hemicellulose** component of the fibrous parts of plants.

xylaric acid the **aldaric acid** derived from **xylose**.

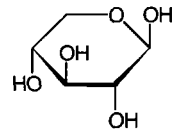
xylE a gene in *Escherichia coli* that encodes a xylose transport protein. A 12-transmembrane-domain protein, it functions as an H^+–xylose symporter. The gene is induced by xylose. Protein product: database code XYLE_ECOLI, 491 amino acids (53.55 kDa). *See also* **sugar transporter**.

xylem the vascular tissue that conducts water and mineral salts from the roots to the aerial parts of a plant and provides it with mechanical support.

xylo+ *or (sometimes before a vowel)* **xyl+** *comb. form indicating the trivial name for* the aldopentose xylose.

xylo- *prefix (in chemical nomenclature)* indicating a particular configuration of a set of three contiguous >CHOH groups, as in the acyclic form of D- or L-xylose. *See* **monosaccharide**.

xylose *symbol*: Xyl; *xylo*-pentose; a constituent of plant polysaccharides (*see* **xylan**); the naturally occurring enantiomer is always D-xylose. The metabolism of xylose in the human is restricted, and most is excreted unchanged in the urine. In clinical chemistry this forms the rationale for the **xylose absorption test**, the most widely used test of carbohydrate absorption.



β-D-pyranose form

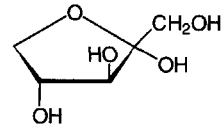
xylose isomerase EC 5.3.1.5; *systematic name*: D-xylose ketol-isomerase; an enzyme that catalyses the reaction:

D-xylose = D-xylulose;

magnesium ions are a cofactor. Example from *Streptomyces olivochromogenes*: database code NRL_3XIA, 377 amino acids (41.90 kDa); 3-D structure known; it is a **beta-barrel** protein.

xylose-1-phosphate uridylyltransferase *see* **UTP–xylose-1-phosphate uridylyltransferase**.

xylulose *symbol*: Xul; *the trivial name for* the ketopentose *threo*-2-pentulose; D-xylulose is the naturally occurring enantiomer.



α-D-xylulose

D-xylulose 5-phosphate the 5-phosphate ester of D-xylulose and a component of the **pentose phosphate pathway**. It is formed from D-ribulose 5-phosphate by ribulose-phosphate 3-epimerase (EC 5.1.3.1); D-xylulose 5-phosphate then reacts with D-ribose 5-phosphate, catalysed by **transketolase**, to give glyceraldehyde 3-phosphate and sedoheptulose 7-phosphate.

X-Y-Z-cell theory a theory describing immunocyte maturation in which the first committed immunocyte, the **X cell**, is transformed by antigen into a memory cell, the **Y cell**, in the primary response, and is further stimulated in the secondary response to become an antibody producer, the **Z cell**.

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Yy

y *symbol for* yocto+ (SI prefix denoting 10^{-24} times).

y *symbol for* **1** amount-of-substance fraction (i.e. mole fraction) or number fraction for gases. *Compare* ***x***. **2** a Cartesian space coordinate, complementary to *x* and *z*.

Y *symbol for* **1** yotta+ (SI prefix denoting 10^{24} times). **2** a residue of the α-amino acid L-tyrosine (alternative to Tyr). **3** a residue of an incompletely specified base in a nucleic-acid sequence that may be either cytosine or thymine. **4** a residue of an unspecified pyrimidine nucleoside (alternative to Pyd). **5** a residue of the minor nucleoside **wyosine** (alternative to W). **6** yield. **7** yttrium.

Y *symbol for* admittance (reciprocal of impedance).

YAC *abbr. for* yeast artificial chromosome.

Yalow, Rosalyn Sussman (1921–), US physicist; Nobel Laureate in Physiology or Medicine (1977) 'for the development of radioimmunoassays of peptide hormones' [prize shared with R. Guillemin and A. V. Schally].

Yb *symbol for* ytterbium.

Y cell *see* **X-Y-Z-cell**.

Y chromosome a **sex chromosome** found only in the **heterogametic** sex and usually different in size from the **X chromosome**. In many animals it carries the testis-determining factor that triggers male embryonic development.

yeast any of a group of unicellular fungi that reproduce asexually – by budding or fission – and sexually – by the production of ascospores. Yeast cells may occur singly or in short chains, and some species produce a mycelium. The term 'yeast' is often used to mean members of the genus *Saccharomyces*, e.g. *S. cerevisiae*), which is an example of a budding yeast, or *Schizosaccharomyces pombe*, which is an example of a fission yeast.

yeast artificial chromosome *abbr.*: YAC; a specialized cloning vector that contains a **centromere**, an autonomously replicating sequence (ARS), a pair of **telomeres**, selectable marker genes, and the fragment of DNA to be cloned. Usually, genomic DNA is digested to produce fragments containing the genes, which are separated by **pulsed field gel electrophoresis**; the large fragments are then ligated into YACs. They are capable of propagation in yeasts, where they function as 'artificial chromosomes', being efficiently replicated. YACs are essential in large mapping projects, such as the Human Genome Project (*see* **HUGO**), as they are stable and can carry vast DNA inserts of 100 to 1000 kbp.

yeast cloning any of a number of methods of cloning using yeast as the host; cloning in yeasts and other microbial eukaryotes has a number of advantages. Expression of eukaryote genes in these organisms is subject to eukaryotic regulatory systems, and the products undergo post-translational modification in contrast to when they are expressed in prokaryotes. Thus, yeast clones are often used for the expression of glycoproteins.

yeast eluate factor *a former term for* **vitamin B_6**.

yeast filtrate factor *a former term for* pantothenic acid. *See* **pantothenate**.

yeast nucleic acid *a former term for* **ribonucleic acid**.

yeast two-hybrid system a system that exploits two hybrid proteins, one containing a protein, X, fused to the GAL4 DNA-binding domain, and the other containing a different protein, Y, fused to the GAL4 activation domain. Plasmids encoding each of the hybrid proteins are introduced together into yeast, which leads to the expression of both hybrids. The system is used to test whether protein Y binds to protein X, for example in investigating the role of newly discovered proteins. If the proteins do bind, the resulting complex will be bound to the upstream activation sequence for the yeast *GAL* genes by the GAL4 DNA-binding domain, and the presence of the GAL4 activation domain will lead to transcriptional activation of the **reporter gene**, i.e. β-galactosidase. The system has the advantage over immunoprecipitation that if Y binds to X, the gene encoding it is already available as a clone. The hybrid containing X is referred to as the **bait**.

yellow enzyme **1 old yellow enzyme**, EC 1.6.99.1; NADPH dehydrogenase; a flavoprotein (FMN in yeast, FAD in plants). **2 new yellow enzyme** *an alternative name for* D-amino-acid oxidase; *see* **amino-acid oxidase**.

yellow marrow *see* **bone marrow**.

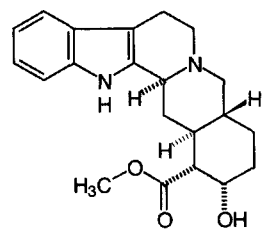
YES **v-*yes*** is the oncogene of the Yamaguchi sarcoma virus, and has a cellular counterpart, **c-*yes***, the product of which is a member of the ***src*** family of non-receptor tyrosine kinases, having a myristoylation site, and SH2, SH3 and tyrosine kinase domains. Example, p61 from *Gallus gallus*: database code YES_CHICK, 541 amino acids (60.79 kDa).

yield *symbol*: Y; a ratio expressing the efficiency of a mass conversion process. The yield coefficient is defined as the amount of cell mass or product formed related to the consumed substrate or to the intracellular ATP production.

yin-yang hypothesis (of biological control) a concept of biological regulation based on the opposing actions of certain cyclic nucleotides. It arises from the observation that hormones or other biologically active substances that promote the cellular accumulation of cyclic GMP produce cellular responses that are antagonistic to ones occurring when the concentration of cyclic AMP is increased in the same tissues or cells. Hence cyclic GMP and cyclic AMP may have opposing or antagonistic regulatory influences in certain biological systems, somewhat analogous to the oriental concept of yin and yang symbolizing a dualism between opposing natural forces.

yocto+ *symbol*: y; SI prefix denoting 10^{-24} times.

yohimbine a complex indole alkaloid, $C_{21}H_{26}N_2O_3$, with α_2-adrenoceptor antagonist activity. It is produced by *Corynanthe johimbe* and *Rauwolfia serpentina*.



Yop *abbr. for Yersinia* outer protein; any of a number of proteins, known as virulence proteins, originally found on the surface of Gram-negative bacteria of the genus *Yersinia*; they are now known to be characteristic of proteins pathogenic to plants, that are secreted by bacteria of genera as diverse as *Pseudomonas*, *Xanthomonas*, and *Erwinia*. They are also produced by animal pathogens such as *Shigella flexneri*, *Salmonella typhimurium*, and *Escherichia coli*. They are secreted by the **type III system**. Unlike other secreted proteins they lack a signal sequence.

yotta+ *symbol*: Y; SI prefix denoting 10^{24} times.

Yphantis method *an alternative name for* **meniscus depletion method (sedimentation equilibrium)**.

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Zz

z *symbol for* zepto+ (SI prefix denoting 10^{-21} times).

z *symbol for* **1** charge number of an ion. **2** a Cartesian space coordinate, complementary to *x* and *y*.

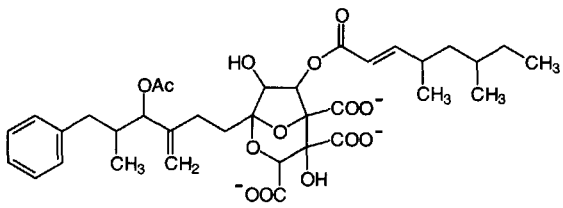
Z *symbol for* **1** zetta+ (SI prefix denoting 10^{21} times). **2** a residue of either of the α-amino acids L-glutamic acid or L-glutamine when the state of amidation is uncertain (alternative to Glx). It may also be used to represent a residue of any other substance, such as 4-carboxy-L-glutamic acid (as alternative to Gla) or 5-oxo-L-proline (as alternative to Glp), that yields glutamic acid on acid hydrolysis of peptides. **3** the **benzyloxycarbonyl** group (alternative to Cbz).

Z *symbol for* **1** proton number. **2** impedance.

(*Z*)- *prefix (in chemical nomenclature)* denoting a geometric isomer in which the highest priority substituent groups, determined according to the Cahn–Ingold–Prelog rules (*see* **sequence rule**), are located on the same side of a double bond. *See also* ***E/Z* convention**.

Zantac *see* **ranitidine**.

zaragozic acid any of a family of closely related fungal metabolites that are potent inhibitors of squalene synthase.



zaragozic acid A

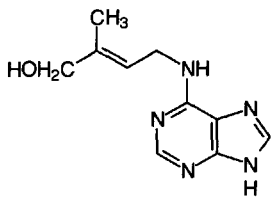
Z-average relative molecular mass *see* **average relative molecular mass**.

Z cell *see* **X-Y-Z cell theory**.

Z disk *or* **Z line** a platelike region of a muscle **sarcomere** to which the plus ends of actin filaments are attached. It is seen as a dark transverse line in micrographs.

Z-DNA *abbr. for* Z form of DNA.

zeatin *trans*-zeatin; (*E*)-2-methyl-4-(1*H*-purin-6-ylamino)-2-buten-1-ol; a plant hormone of the **cytokinin** class. Its derivative, *trans*-zeatin riboside (N^6-(*trans*-4-hydroxy-3-methyl-*cis*-2-buten-1-yl)adenosine) is also a cytokinin. The *cis* form is a rare component in some RNA structures.



***trans*-zeatin-producing protein** an isopentenyl transferase (dimethylallyl transferase) of sub-subclass EC 2.5.1.–. It introduces the isopentenyl moiety (2-methylbut-2-en-1-ol group) into zeatin. Example from *Burkholderia solanacearum* (*Pseudomonas solanacearum*): database code IPT_BURSO, 238 amino acids (26.41 kDa).

zebrafish *Brachydanio rerio*; a small, highly fertile species of characinoid teleost fish with a shiny blue body and four longitudinal yellowish stripes along its sides. It is much used in studies on the molecular biology of differentiation and development in metazoan animals.

Zeeman effect the splitting of a single line in a spectrum, indicative of the degeneration of the excited state of a particular chromophore, into two or more components of slightly different wavelengths brought about by the application of an external magnetic field. [After Pieter Zeeman (1865–1943), Dutch physicist.]

zein the principal storage protein of maize (corn) seeds. It is relatively deficient in the essential amino acids lysine and tryptophan, and tryptophan deficiency can occur in human populations dependent on maize as the major protein source. The zein genes are clustered. Example, an α zein from maize: database code ZEAW_MAIZE, 261 amino acids (28.43 kDa)

zeolite any of a family of porous, naturally occurring (or processed) alkali metal- or alkaline earth-aluminium silicates that show ion-exchange properties. They may be used for water softening or as molecular sieves. —**zeolitic** *adj.*

zepto+ *symbol*: z; SI prefix denoting 10^{-21} times.

zero-order kinetics kinetics shown by a **zero-order reaction**.

zero-order reaction a chemical reaction whose velocity is independent of the concentration of one or more of the reactants. *See* **order of reaction**.

zeroth law of thermodynamics *see* **thermodynamics, laws of**.

zervamicin *see* **peptaibophol**.

zeta *symbol*: ζ (lower case) *or* Z (upper case); the sixth letter of the Greek alphabet. For uses *see* **Appendix A**.

zeta potential *symbol*: ζ; the potential at the surface of shear of a charged particle; for macromolecular ions it is the potential at the surface of the **hydrodynamic particles** formed by such ions.

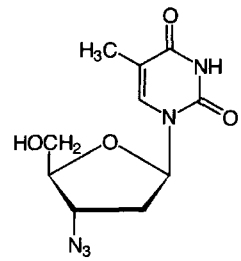
zeta protein *an alternative name for* cellular **fibronectin**.

zetta+ *symbol*: Z; SI prefix denoting 10^{21} times.

zeugmatography a technique in which the addition of carefully controlled inhomogeneous magnetic fields enables measurements of **nuclear magnetic resonance** (NMR) to be made at selected regions of heterogeneous samples and hence the formation of two-dimensional maps of the distribution of almost any property measurable by NMR.

Z form of DNA *abbr.* Z-DNA or DNA-Z; a form of DNA consisting of a left-handed double helix in which the pyrimidine residues are always in the *anti* orientation and the purine residues in the *syn*. So-called because of the zig-zag appearance of its conformation. *See also* **A form** (def. 1), **B form**, **C form**.

zidovudine 3′-azido-3′-deoxythymidine (*abbr.*: AZT); an analogue of thymidine, the phosphorylated form of which is an inhibitor of **reverse transcriptase** in **retroviruses**; it also terminates DNA synthesis. Zidovudine undergoes phosphorylation in human T cells to a nucleoside 5′-triphosphate, which competes with thymidine triphosphate (TTP) and serves as a chain-terminating inhibitor of **HIV** reverse transcriptase. It is used clinically to treat patients with HIV infection and AIDS. *Proprietary name*: Retrovir.



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Zimm–Crothers viscometer a modified **Couette viscometer** in which the inner cylinder is a self-centring float containing a steel pellet. The inner cylinder is caused to rotate by an external rotating magnetic field, the speed of rotation being dependent, *inter alia*, on the viscosity of the fluid. The instrument only measures the viscosity of a sample relative to a standard.

Zimmermann reaction the reaction of *m*-nitrobenzene in strongly alkaline solution with the methylene group at position 16 in 17-ketosteroids to give a purple colour with an absorption maximum at 520 nm. It may be used to estimate such steroids.

Zimm plot a graphical double extrapolation used to analyse most macromolecular light-scattering data. Measurements are made of Kc/R_θ at various concentrations as a function of the scattering angle, 2θ, where K is an optical constant, c is the concentration, and R_θ is the Rayleigh ratio. A series of plots of Kc/R_θ against $(\sin^2\theta + K'c)$ are made, where K' is an arbitrary constant chosen to provide a convenient spread. The data are then extrapolated separately to $c = 0$ and $\theta = 0$. The intersection of the two extrapolated curves yields the relative molecular mass.

zinc *symbol* Zn; a metal of group 12 of the IUPAC **periodic table**; relative atomic mass 65.38; atomic number 30. The principal ore is zincblende, ZnS. Its oxidation state is Zn(II). Zinc oxide is used as an antiseptic. Naturally occurring nuclides include (relative abundance follows each) $^{64}_{30}$Zn (48%), $^{66}_{30}$Zn (28%), $^{68}_{30}$Zn (18%). Radionuclides include **zinc-62**, **zinc-65**, and **zinc-72**. Dietary deficiency in the rat is manifested by retarded growth, alopecia, and lesions in the skin, esophagus, and cornea. Deficiency is rare in normal individuals, but can manifest itself in alcoholics and in patients with renal disease or malabsorption. Zn^{2+} is an essential cofactor for many enzymes. Recent work suggests zinc is bactericidal.

zinc-62 the artificial radioactive nuclide $^{62}_{30}$Zn; it emits a positron (β^+ particle) (0.66 MeV), and γ-radiation of four energies (0.041, 0.25, 0.51, and 0.60 MeV). It has a half-life of 9.26 h.

zinc-65 the artificial radioactive nuclide $^{65}_{30}$Zn; it emits a positron (β^+ particle) (0.325 MeV) and γ-radiation (1.12 MeV). It has a half-life of 244.1 days.

zinc-72 the artificial radioactive nuclide $^{72}_{30}$Zn; it emits an electron (β^- particle) (0.3 MeV) and γ-radiation of three energies (0.016, 0.145, and 0.192 MeV). It has a half-life of 1.938 days.

zinc finger a polypeptide motif present in many DNA-binding proteins and having the consensus sequence

$$\text{-}CX_{2\text{–}4}CX_3FX_5LX_2HX_3H\text{-}.$$

The motif takes its name from its zinc-binding site, which forms a finger-like loop in the peptide, also described as the **Cys_2/His_2 finger**, the Cys and His residues coordinating a zinc ion. Zinc fingers are most notably present in **transcription factors** (e.g. TFIIIA and SP1), which have several repeats of the motif; they are required for binding of the transcription factor to DNA. *See also* **Appendix E**.

ZIP *abbr. for* the leucine zipper domain. *See also* **bZIP**.

Z line *another name for* **Z disk**.

Zn *symbol for* zinc.

Zollinger–Ellison syndrome a disease syndrome caused by excessive secretion of **gastrin**, either from (type 1) **G-cell** hyperplasia in the antrum of the stomach, or from (type 2) a benign or malignant pancreatic islet tumour (**gastrinoma**). The manifestations include multiple peptic ulcers, or peptic ulcers in unusual sites, with a marked tendency to bleeding, often associated with hyperparathyroidism. [After Robert M. Zollinger (1903–) and Edwin H. Ellison (1918–70).]

zona adherens *see* **desmosome**.

zona fasciculata *see* **adrenal gland**.

zona glomerulosa *see* **adrenal gland**.

zonal centrifugation *an alternative name for* **density-gradient centrifugation**.

zonal centrifuge a centrifuge designed to allow large-scale and continuous fractionation by **density-gradient centrifugation**.

zonal rotor any centrifuge rotor of high capacity used preparatively in a **zonal centrifuge**.

zona occludens *an alternative name for* **tight junction**.

zona pellucida sperm-binding protein *abbr.*: ZP; any of several sulfated transmembrane glycoproteins (ZP1, ZP2, ZP3) that together form the zona pellucida of the oocyte. ZP3 functions as a sperm receptor. Example ZP3α from *Sus scrofa*: database code ZPB_PIG, 536 amino acids (59.33 kDa).

zona reticularis *see* **adrenal gland**.

zone electrophoresis a method of **electrophoresis** in which the protein (or other) solution is placed at the starting position as a thin band or spot in an inert supporting medium (paper, starch gel, polyacrylamide gel, etc.), containing buffer solution. An electric potential is then applied to the supporting medium, causing the proteins (or other substances) to migrate to give distinct bands or zones. These may be located *in situ* by staining, light absorption, etc., or by analysis after elution of discrete pieces of the supporting medium.

zone precipitation a technique in which protein is precipitated as a zone in a gel-filtration column by eluting with a gradient of a protein-precipitating agent. *See* **gel-permeation chromatography**.

zone spreading the broadening of a zone in electrophoresis or chromatography due to eddy currents or other disturbances in the supporting medium.

zoo blot a method for detecting conservation of DNA sequence during evolution. A segment of DNA being investigated is used as a probe to hybridize against a series of DNA samples from various species, and hence establish whether the DNA sequence has been conserved during evolution.

zoonosis (*pl.* **zoonoses**) any disease that can be transmitted to humans from other animals in natural circumstances.

zooplankton *see* **plankton**.

zootoxin any poisonous substance formed by animal cells.

Zovirax *a proproetary name for* **acyclovir**.

Zr *symbol for* zirconium.

Z scheme a term sometimes applied to two-system photosynthetic light reactions, utilizing both **photosystems** I and II. It is descriptive of the mode of photosynthesis used by higher plants and algae, and by cyanobacteria. The way in which it is normally plotted, with redox potential (on the ordinate) against time, shows there is a sudden jump on excitation by a photon of a reaction centre, followed by a slow decline through electron transport components, and gives a (horizontal) Z-like appearance, hence the name.

zuotin a nuclear Z-DNA-binding protein of *Saccharomyces cerevisiae*. Example from yeast: database code ZUO1_YEAST, 433 amino acids (49.02 kDa).

zwischenferment *an obsolete term for* an enzyme–coenzyme complex of which **glucose-6-phosphate dehydrogenase** is the apoenzyme.

Zwittergent *the proprietary name for* any of a group of zwitterionic detergents containing a **betaine** and a sulfonate group; such molecules retain their amphoteric (zwitterionic) properties over a very wide range of pH. The formula is *n*-alkyl *N*,*N*-dimethyl-3-ammonio-1-propanesulfonate. In Zwittergent 3-08, alkyl is octyl (CMC 330 mM); 3-10, decyl (aggregation number 41, CMC 25–40 mM); 3-12, dodecyl (aggregation number 55, CMC 2–4 mM); 3-14, tetradecyl (aggregation number 83, CMC 0.1–0.4 mM); 3-16, hexadecyl (aggregation number 155, CMC 0.01–0.06 mM).

zwitterion *an alternative name for* **dipolar ion**.

zwitterionic buffer a **buffer solution** whose acid or base component is a zwitterion (i.e. **dipolar ion**). The term is used especially of solutions of **Good buffer substances** and newer equivalents.

zygote any fertilized ovum before it has undergone cleavage. —**zygotic** *adj.*

zygotene the second phase of prophase I in **meiosis**.

zymase the name originally given to the heat-labile, nondif-

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fusible fraction of a crude extract of brewers' yeast that, with the addition of the heat-stable, diffusible fraction (i.e. **co-zymase**), would enable the alcoholic fermentation of glucose to occur in a cell-free system. It was later shown to consist of a mixture of enzymes, including those of the **glycolytic pathway**.

zymogen *or* **proenzyme** *or (formerly)* **proferment** the inactive precursor of an enzyme, often convertible to the enzyme by partial proteolysis. The term is applied especially to catalytically inactive forms of pancreatic enzymes such as trypsinogen, chymotrypsinogen, proelastase, and procarboxypeptidase; these are cleaved to remove a peptide to produce the active enzyme after their secretion from granules (**zymogen granules**) in the acinar cells of the pancreas.

zymogen granule a membrane-bound, cytoplasmic **secretory granule** visible by light microscopy. Zymogen granules are formed in the Golgi apparatus of enzyme-secreting cells and serve to store a **zymogen**. The term is used especially of a secretory granule containing the proenzyme of a digestive enzyme.

zymogram **1** any record of a **zone electrophoresis** separation in which enzymes in a sample have been separated and their positions, and relative amounts, revealed by an **activity stain**. **2** any table showing the results of carbohydrate-fermentation tests carried out in the process of identifying a microorganism.

zymohexase *an obsolete name for* **fructose bisphosphate aldolase**.

zymology the science dealing with fermentations. —**zymological** *adj.*; **zymologist** *n.*

zymosan a crude preparation of yeast cell walls, consisting chiefly of polysaccharide, that activates the alternative pathway of the complement system in the presence of properdin.

zymosterol cholesta-8,24-dien-3β-ol; a sterol present in yeasts e.g. *Candida albicans*, *Saccharomyces cerevisiae*.

zymurgy the branch of chemistry dealing with the applications of fermentation processes, especially to brewing and wine-making.

zyxin a protein component of cell substratum and cell–cell adherens junctions. It is a component of adhesion plaques and the termini of stress fibres near the point of association with the cytoplasmic face of the adhesive membrane and interacts with α-actinin. Example from *Gallus gallus*: database code ZYX_CHICK, 542 amino acids (58.53 kDa).

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Appendix A

The Greek alphabet and Greek characters used as symbols

The Greek alphabet

Name	Capital letter	Lower-case letter	English transliteration
alpha	A	α	a
beta	B	β	b
gamma	Γ	γ	g
delta	Δ	δ	d
epsilon	E	ε	e
zeta	Z	ζ	z
eta	H	η	ē *or* e
theta	Θ	θ	th
iota	I	ι	i
kappa	K	κ	k
lambda	Λ	λ	l
mu	M	μ	m
nu	N	ν	n
xi	Ξ	ξ	x
omicron	O	ο	o
pi	Π	π	p
rho	P	ρ	r
sigma	Σ	σ or ς (at end of word)	s
tau	T	τ	t
upsilon	Y	υ	u
phi	Φ	φ	ph
chi	X	χ	kh
psi	Ψ	ψ	ps
omega	Ω	ω	ō *or* o

Single-character symbols

α (*or* α) **1** a heavy chain of immunoglobulin A. **2** maximal agonist effect. **3** alpha particle.

α (*or α*) **1** angle of optical rotation (a_{obs} is used for observed rotation and [*a*] for specific optical rotation *or* specific optical rotatory power; a_m is used for molar optical rotatory power). **2** absorptance. **3** (linear) napierian absorption coefficient. **4** Bunsen coefficient. **5** partition coefficent. **6** plane angle. **7** *(in organic chemical nomenclature)* a locant for a substituent on the first atom from the atom carrying the principal function in an acyclic structure or in a side chain attached to a cyclic structure. **8** an anomeric configuration (of a sugar molecule or residue; *see* **anomer**). **9** winding number (of a helical duplex DNA molecule).

β (*or* β) beta particle (β^- is used for an electron and β^+ for a positron).

β (*or β*) **1** buffer value. **2** pressure coefficient. **3** plane angle. **4** *(in organic chemical nomenclature)* a locant for a substituent on the second atom from the atom carrying the principal function in an acyclic structure or in a side chain attached to a cyclic structure. **5** an anomeric configuration (of a sugar molecule or residue; *see* **anomer**). **6** number of secondary turns (in an unconstrained helical duplex DNA molecule).

γ (*or* γ) a heavy chain of immunoglobulin G. **2** a photon of gamma radiation. **3** *(obsolete)* microgram (μg now used).

γ (*or γ*) activity coefficient (γ_c is used for activity coefficient when expressed on a concentration basis, γ_m when expressed on a molality basis, γ_x when expressed on a mole fraction basis, and $\gamma_\pm$ is used for mean ionic activity coefficient). **2** electrical conductivity (alternative to κ or σ). **3** mass concentration *or* mass density (alternative to ρ). **4** plane angle. **5** surface tension *or* interfacial tension (alternative to σ). **6** gyromagnetic ratio. **7** *(in organic chemical nomenclature)* a locant for a substituent on the third atom from the atom carrying the principal function in an acyclic structure or in a side chain attached to a cyclic structure.

δ (*or* δ) **1** a heavy chain of immunoglobulin D. **2** (*in mathematics*) an infinitesimal change or difference.

δ (*or δ*) **1** chemical shift. **2** number fraction. **3** *(in organic chemical nomenclature)* a locant for a substituent on the fourth atom from the atom carrying the principal function in an acyclic structure or in a side chain attached to a cyclic structure.

Δ (*or* Δ) (*in mathematics*) a finite change or difference.

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Appendix A

Δ (*or Δ*) (*in older organic chemical nomenclature*) a locant for a double bond (a right superscript number designates the lower-numbered carbon atom; see **fatty-acid nomenclature**); no longer recommended for denoting unsaturation in names of individual compounds although it may still be used in generic terms (e.g. Δ^5-steroid) and in symbols (e.g. Δ_2Ach).

ε (*or* ε) a heavy chain of immunoglobulin E.

ε (*or ε*) **1** molar (decadic) absorption coefficient. **2** permittivity (ε_r is used for relative permittivity and ε_0 for permittivity of vacuum). **3** *(in organic chemical nomenclature)* a locant for a substituent on the fifth atom from the atom carrying the principal function in an acyclic structure or in a side chain attached to a cyclic structure. **4** (*in chemical nomenclature*) hapticity of a ligand (less common alternative to *η*; *see* **hapto**).

ε_a degree of activation (of an enzymic reaction).

ε_i degree of inhibition (of an enzymic reaction).

ε_s^v elasticity coefficient (of a specific enzymic step in a metabolic system).

ζ (*or ζ*) electrokinetic potential *or* zeta potential.

η (*or η*) **1** viscosity (alternative to *μ*). **2** *(in chemical nomenclature)* hapticity (of a ligand; more common alternative to *ε; see* **hapto**).

θ (*or θ*) **1** Bragg angle (*see* **Bragg's law**). **2** (*in surface chemistry*) contact angle. **3** plane angle. **4** torsion angle (in a linear sequence of four attached atoms; alternative to *ω*). **5** Celsius temperature (alternative to *t*).

Θ_m melting temperature (alternative to T_m *or* t_m).

[Θ] molar ellipticity.

κ (*or* κ) one type of light chain of any class of immunoglobulin (the other being λ).

κ (*or κ*) **1** electrical conductivity (alternative to *γ* or *σ*). **2** electrolytic conductivity *or* (*formerly*) specific conductance. **3** molar napierian absorption coefficient. **4** magnetic susceptibility (alternative to *χ*).

λ (*or* λ) **1** one type of light chain of any class of immunoglobulin (the other being κ). **2** *(obsolete)* microlitre (μl now used).

λ (*or λ*) **1** (*in thermodynamics*) absolute activity (*see* **activity**, def. 4). **2** disintegration constant *or* decay constant. **3** wavelength. **4** thermal conductivity (alternative to *k*).

Λ (*or Λ*) molar conductivity (of an electrolyte).

μ (*or* μ) a heavy chain of immunoglobulin M. **2** micro+ (SI prefix denoting 10^{-6} times). **3** (*obsolete*) micron (now called micrometre; symbol: μm).

μ (*or μ*) **1** *(in chemical nomenclature)* a bridging ligand. **2** viscosity (alternative to *η*). **3** chemical potential (μ^o *or* $\mu^{\ominus}$ is used for standard chemical potential and $\tilde{\mu}$ is used for electrochemical potential). **4** electric mobility (alternative to *u*). **5** *(in magnetism)* permeability (μ_r is used for relative permeability). **6** magnetic dipole moment (bold italic) (alternative to ***m***). **7** electric dipole moment (bold italic) (alternative to ***p***).

μ_0 permeability of vacuum (a fundamental physical constant).

μ_B Bohr magneton (a fundamental physical constant).

μ_e electron magnetic moment (a fundamental physical constant).

μ_N nuclear magneton (a fundamental physical constant).

μ_p proton magnetic moment (a fundamental physical constant).

ν (*or ν*) **1** stoichiometric number (of a chemical reactant). **2** frequency (alternative to *f* for electromagnetic radiation). **3** kinematic viscosity. **4** endocyclic torsion angle (in a sugar residue).

ξ **1** (*in organic chemical nomenclature*) unknown configuration at a chiral centre. **2** extent of reaction.

$\dot{\xi}$ rate of conversion.

π (*or* π) a transcendental number that is the ratio of the circumference of a circle to its diameter (3.141 592 653 59...).

π (*or π*) **1 pros**. **2** (*or* π^s) surface pressure.

Π (*or Π*) **1** osmotic pressure (Π_D may be used to represent colloid osmotic pressure). **2** binding potential (of a ligand).

ρ (*or ρ*) **1** density *or* mass density (ρ_A *or* ρ_S is used for surface density). **2** mass concentration *or* mass density (alternative to *γ*). **3** radiant energy density (alternative to *w*). **4** charge density. **5** resistivity.

σ (*or σ*) **1** surface tension *or* interfacial tension (alternative to *γ*). **2** electrical conductivity (alternative to *γ or κ*). **3** wavenumber in a medium. **4** surface charge density. **5** *(in surface chemistry)* area per molecule. **6** *(in nuclear magnetic resonance spectroscopy)* shielding constant. **7** superhelix density (of a helical duplex DNA molecule).

Σ (*or* Σ) *(in mathematics)* a summation sign.

τ (*or τ*) **1 tele**. **2** bond angle. **3** relaxation time *or* time constant (alternative to *T*). **4** transmittance *or* transmission factor (alternative to *T*). **5** mean life. **6** number of superhelical turns (in a helical duplex DNA molecule).

φ (*or φ*) **1** osmotic coefficient (φ_m is used for osmotic coefficient when expressed on a molality basis and φ_x when expressed on a mole fraction basis). **2** electric potential (alternative to *V*). **3** fluidity. **4** plane angle. **5** phase difference. **6** volume fraction. **7** Dalziel coefficient. **8** torsion angle (from the anomeric carbon atom to the oxygen atom of a glycosidic bond). **9** quantum yield (alternative to *Φ*). **10** winding angle (of intercalated helical DNA).

Φ (*or Φ*) **1** heat flow rate. **2** radiant power *or* radiant (energy) flux (alternative to *P*). **3** magnetic flux. **4** potential energy (alternative to E_p or *V*). **5** quantum yield (alternative to *φ*).

χ (*or χ*) **1** electronegativity. **2** magnetic susceptibility (alternative to *κ*; χ_m is sometimes used, but it should be reserved for molar magnetic susceptibility). **3** surface electric potential. **4** exocyclic torsion angle (in a sugar residue).

ψ (*or ψ*) **1** replacement of the –CO–NH– group in a peptide by another (indicated) grouping. **2** torsion angle (from the oxygen atom of a glycosidic bond to the glycosylated molecule). **3** wavefunction (alternative to *Ψ*).

Ψ (*or Ψ*) **1** a residue of the ribonucleoside pseudouridine (alternative to Ψrd). **2** electric flux. **3** wave function (alternative to *ψ*).

ω (*or ω*) **1** angular frequency. **2** angular velocity. **3** solid angle. **4** torsion angle (in a linear assembly of four attached atoms; alternative to *θ*). **5** (*in organic chemical nomenclature*) a locant for the terminal atom or group in an acyclic organic compound.

Ω (*or* Ω) ohm.

Ω (*or Ω*) solid angle.

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Multi-character biochemical symbols commencing with a Greek character

αLnn the linolenoyl *or* (9,12,15)-linolenoyl *or* (*formerly*) α-linolenoyl (i.e. (*all-Z*)-octadeca-9,12,15-trienoyl) group (alternative to Lnn).

βAad a residue of the β-amino acid L-β-aminoadipic acid (i.e. L-3-aminohexanedioic acid).

βAla a residue of the β-amino acid β-alanine (i.e. 3-amino-propanoic acid).

γLnn the (6,9,12)-linolenoyl *or* (*formerly*) γ-linolenoyl (i.e. (*all-Z*)-octadeca-6,9,12-trienoyl) group.

Δ_2Ach the (*all-Z*)-eicosa-8,11-dienoyl group.

Δ_3Ach the (*all-Z*)-eicosa-5,8,11-trienoyl group.

Δ_4Ach the arachidonoyl (i.e. (*all-Z*)-eicosa-5,8,11,14-tetra-enoyl) group.

ΔPam the palmitoleoyl (i.e. (*Z*)-hexadec-9-enoyl) group.

εAcp *see* **εAhx**.

εAhx *or* (*formerly*) **εAcp** a residue of the ε-amino acid 6-aminohexanoic acid (formerly known as ε-amino-caproic acid).

Ψrd a residue of the ribonucleoside pseudouridine (alternative to Ψ).

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Appendix B

Nomenclature publications

Introduction

Brief details are provided below of a selection from the considerable number of publications available on nomenclature and symbolism that are of possible interest to biochemists, biological chemists, clinical chemists, and molecular biologists. The majority of these publications are in the form of approved recommendations from the International Union of Biochemistry (IUB) or its successor the International Union of Biochemistry and Molecular Biology (IUBMB) through their Nomenclature Committees (respectively NC–IUB or NC–IUBMB), from the International Union of Pure and Applied Chemistry (IUPAC), or from IUPAC and IUBMB together through their Joint Commission on Biochemical Nomenclature (JCBN); on occasions the recommendations have been issue by IUPAC in conjunction with IUBMB and the International Union of Pure and Applied Biophysics (IUPAB) or by IUPAC jointly with the International Federation of Clinical Chemistry (IFCC). The full titles of the relevant nomenclature bodies to which the listed publications are attributable have generally been omitted for brevity.

This Appendix has been updated and expanded for the revised edition of the Dictionary. Now incorporated are details of significant nomenclature documents published and made available up to the end of August 1999 (or in certain instances known to be in preparation at that date). Furthermore, the interval following the compilation of the original version of this appendixhas seen a considerable increase in the number of specific biochemical and chemical nomenclature recommendations whose full texts have been converted to versions readable on the Internet via the World Wide Web (WWW), and so their current uniform resource locators (URLs) have been added where appropriate. All such recommendations are also currently accessible (directly or indirectly) through links from either of the following URLs:

`www.chem.qmw.ac.uk/iubmb/`
(IUBMB Biochemical Nomenclature home page)
`www.chem.qmw.ac.uk/iupac/`
(IUPAC Chemical Nomenclature home page)

It will be appreciated that, in order for information as up-to-date as possible to be given in this Appendix, details have been included of a number of nomenclature documents that became available too recently for their contents to be taken into consideration during the compilation of this Dictionary.

Manuals and Compendia

These are volumes covering major subject areas, the majority being assemblages either of previously published nomenclature documents on specific topics or of items extracted from such documents. Some duplication of content between them has inevitably occurred. They are commonly known by the colour of their covers.

1 [The Blue Book] IUPAC (1979). *Nomenclature of organic chemistry — sections A, B, C, D, E, F and H — 1979 edn* (ed. J. Rigaudy and S. P. Klesney). Pergamon Press, Oxford.

A collection of several previously published separate sets of rules and recommendations, reprinted with correction of material errors. The section headings are listed in item 34. *See also* item 6.

URL for section H (isotopically modified compounds):

`http://www.chem.qmw.ac.uk/iupac/sectionH/`

2 [The Red Book] IUPAC (1990). *Nomenclature of inorganic chemistry — recommendations 1990* (ed. G. J. Leigh). Blackwell Scientific Publications, Oxford.

Recommendations conceived as being Part I of a third edition of the Red Book and mainly concerned with the fundamental areas of inorganic chemistry.

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A series of chapters includes: the rules for naming simple molecular entities; oxoacids and their derivatives; coordination compounds; and simpler boron compounds. The chapter headings are listed in item 34. Further volumes, which will deal with more specialized aspects of the subject, are expected to be published in about 2001.

3 [The Purple Book] IUPAC (1991). *Compendium of macromolecular nomenclature* (ed. W. V. Metanomski). Blackwell Scientific Publications, Oxford.

A collection of reprints of previously published sets of recommendations providing definitions of terms relating to polymers and rules for naming them based on structure or source. The chapter headings are listed in item 34.

4 [The White Book] NC–IUBMB (1992). *Biochemical nomenclature and related documents — a compendium, 2nd edn* (ed. C. Liébecq). Portland Press, London.

An assemblage of a considerable number of previously published sets of recommendations issued by various nomenclature bodies of IUB, IUPAC, or IUB and IUPAC jointly, together with excerpts from the newsletters of the biochemical nomenclature committees. Most of the nomenclature documents contained in the first (1978) edition of the compendium are either reprinted (with updates where appropriate) or replaced by revised versions, and to these is added a number of new sets of recommendations published between 1978 and 1989. Also included are a list of titles of additional biochemical nomenclature documents (including those printed in the first edition of the compendium but not in this one) and an extensive list of titles of other nomenclature and reference publications of possible interest to biochemists. The main contents are listed in item 34.

The full texts of the individual recommendations in this compendium are available as World Wide Web versions or (if not superseded) are in course of being converted into this form; the titles and URLs of those currently accessible are included in a list of WWW versions of current biochemical nomenclature recommendations given at:

`http://www.chem.qmw.ac.uk/iubmb/nomenclature/`

5 [The Green Book] IUPAC (1993). *Quantities, units and symbols in physical chemistry,* 2nd edn (ed. I. M. Mills, T. Cvitaš, K. H. Homann, N. Kallay, and K. Kuchitsu). Blackwell Scientific Publications, Oxford.

The contents are drawn from the resolutions or recommendations of a number of international bodies concerned with the definition and use of physical quantities and units. Included are: the definitions and mandatory symbols for the base and derived units forming the International System (SI), with the names and symbols for SI prefixes signifying decimal multiples and submultiples of SI units; factors for conversion of units from a variety of other systems to the corresponding SI units; sets of tables containing the internationally recommended names and symbols for the base and derived physical quantities most likely to be used by chemists and biochemists, with brief definitions and the corresponding coherent SI units; recommended mathematical symbols; a table of fundamental physical constants; and tables of the properties of chemical elements, nuclides, and particles.

6 [The Blue Book II] IUPAC (1993). *A guide to IUPAC nomenclature of organic compounds — recommendations 1993* (ed. R. Panico, W. H. Powell, and J.-C. Richer). Blackwell Science, Oxford.

For use in conjunction with item 1; it outlines the main principles of organic nomenclature as described in that volume, and presents important changes (published and hitherto unpublished) agreed upon since.

7 [The Silver Book] IUPAC and IFCC (1995). *Compendium of terminology and nomenclature of properties in clinical laboratory sciences (recommendations 1995)* (ed. J. C. Rigg, S. S. Brown, R. Dybkær, and H. Olesen). Blackwell Science, Oxford.

A guide towards a more uniform way of reporting information in clinical sciences, particularly quantitative information in clinical chemistry; it was compiled by harmonizing, updating where appropriate, and consolidating a number of previously published documents and recommendations not readily accessible. Derived physical or chemical quantities are analysed into their dimensions, with the aim of facilitating the interpretation of many of the older names of quantities used in this sphere and the recalculation of data expressed in older units.

8 [The Gold Book] IUPAC (1997). *Compendium of chemical terminology — IUPAC recommendations, 2nd edn* (ed. A. D. McNaught and A. Wilkinson). Blackwell Science, Oxford.

An alphabetical listing of nearly 7000 terms covering the whole range of chemistry. The terms have been selected from a considerable number of internationally approved nomenclature documents and compilations published up to the end of 1995, including all IUPAC recommendations, together with some particularly significant material from 1996. Brief but authoritative definitions are given for each term, together with references to the source documents.

9 [The Orange Book] IUPAC (1998). *Compendium of analytical nomenclature, 3rd edn — definitive rules 1997* (ed. J. Inczédy, T. Lengyel, and A. M. Ure). Blackwell Science, Oxford.

A compilation of previously published documents. The chapter headings are listed in item 34.

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Appendix B

Enzyme list

10 NC-IUBMB (1992). *Enzyme nomenclature – recommendations 1992* (ed. E. C. Webb). Academic Press, San Diego.

A nomenclature and classification of enzymes according to the chemical reactions they catalyse, with systematic names, code numbers, and recommended short names assigned to each one. This, the sixth complete edition of the recommendations, lists 3196 individual enzymes (an increase of 29% on the number in the fifth (1984) edition). Included is a second printing, with corrections, of the contents of item 14 [a further correction is given at: *European Journal of Biochemistry*, 1993, **213**, 3, footnote 1].

Supplements giving corrections and additions to the enzyme list are published periodically, the following having appeared in print by the end of August 1999: Supplement (1994) *European Journal of Biochemistry*, **223**, 1–5; Supplement 2 (1995) *ibidem*, **232**, 1–6; Supplement 3 (1996) *ibidem*, **237**, 1–5; Supplement 4 (1997) *ibidem*, **250**, 1–6; Supplement 5 (1999) *ibidem*, **264**, 610–650. Supplement 6 (1999) is expected to appear in print at a later date. Except for Supplement 5, these supplements all relate to enzyme subclass EC 3.4 (peptidases).

World Wide Web versions of Supplement 5 and of a consolidated list containing the full amended text of subclass EC 3.4 are available.

URL: `http://www.chem.qmw.ac.uk/iubmb/enzyme/`

Conversion of the remaining text of *Enzyme nomenclature* to a consolidated WWW version is expected to be completed by the end of 2000; changes in format for this version will include expansion of the comments section for each enzyme, more complete and up-to-date references, and citation of references at the end of each entry.

Documents on specific topics

A selection of nomenclature documents on specific topics, most of them recently published, is given below. Information from some of them has been incorporated into certain of the compendia mentioned above.

All the recommendations by IUPAC and JCBN have been published initially in *Pure and Applied Chemistry*, and all the NC–IUB or NC–IUBMB recommendations have been first published in *European Journal of Biochemistry* (where the JCBN recommendations have usually also been published). Although many of these recommendations have been reprinted in other research journals, only the initial publication is given for each of the documents itemized below; all appearances of the JCBN, NC–IUB, or NC–IUBMB documents, including any in translation, are enumerated in the publications list cited in item 33.

11 Baron, D. N., Moss, D. W., Walker, P. G., and Wilkinson, J. H. (1971). Abbreviations for names of enzymes of diagnostic importance. *Journal of Clinical Pathology*, **24**, 656–657.

A list of two- or three-letter abbreviations (strictly contractions) of the names of enzymes frequently assayed in clinical biochemistry laboratories. The abbreviations were devised to standardize their use in clinical reports and to facilitate processing of assay data by computer.

12 NC–IUB (1979). Units of enzyme activity – recommendations 1978. *European Journal of Biochemistry*, **97**, 319–320. Corrections: *ibidem*, 1980, **104**, 1–4.

13 Eicosanoid Nomenclature Committee (1989). Eicosanoid nomenclature. *Prostaglandins*, **38**, 125–133.

Proposals regarding a systematic leukotriene nomenclature and suggestions on the nomenclature of enzymes involved in eicosanoid metabolism. The spelling 'eicosanoid' is favoured in preference to 'icosanoid'. The ad hoc committee putting forward these proposals and suggestions was constituted by the IUB as an advisory panel but the recommendations have not been adopted by NC–IUB or NC–IUBMB.

14 NC–IUB (1991). Nomenclature of electron-transfer proteins — recommendations 1989 (ed. G. Palmer and J. Reedijk). *European Journal of Biochemistry*, **200**, 599–611. Corrections: *ibidem*, 1993, **213**, 2–3. *See also* item 10.

15 IUPAC (1994). Glossary of terms used in physical organic chemistry, 2nd edn (IUPAC recommendations 1994) (ed. P. Müller). *Pure and Applied Chemistry*, **66**, 1077–1184.

URL: `http://www.chem.qmw.ac.uk/iupac/gtpoc/`

16 JCBN (1994). Recommendations for nomenclature and tables in biochemical thermodynamics (recommendations 1994) (ed. R. A. Alberty). *Pure and Applied Chemistry*, **66**, 1641–1666.

17 IUPAC (1994). Glossary of bioanalytical nomenclature — part I: general terminology, body fluids, enzymology, immunology (IUPAC recommendations 1994) (ed. C. A. Burtis and T. A. Geary). *Pure and Applied Chemistry*, **66**, 2587–2604.

Definitions taken from IUPAC, IUB, and IFCC nomenclature documents and other sources to form a compilation useful for practitioners of clinical chemistry.

18 NC–IUBMB (1994). A nomenclature of junctions and branchpoints in nucleic acids — recommendations 1994 (ed. D. M. J. Lilley, R. M. Clegg, S. Diekmann, N. C. Seeman, E. von Kitzing, and P. Hagerman). *European Journal of Biochemistry*, **230**, 1–2.

19 Stewart, A. (ed.) (1995) Genetic nomenclature guide — including information on genomic databases. *Trends in Genetics*, **11**(3), suppl. A summary of the most important rules and guidelines for the genetic

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nomenclature of 15 favoured research organisms used by geneticists and developmental biologists.

20 IUPAC (1995). Glossary of class names of organic compounds and reactive intermediates based on structure (IUPAC recommendations 1995) (ed. G. P. Moss, P. A. S. Smith, and D. Tavernier). *Pure and Applied Chemistry*, **67**, 1307–1375.

A glossary of terms used to denote classes of (mostly organic) compounds, substituent groups, and reactive intermediates, in contrast to individual compounds. The terms have been selected both from IUPAC or IUB/IUBMB nomenclature publications and from the chemical literature.

URL: `http://www.chem.qmw.ac.uk/iupac/class/`

21 IUPAC and IFCC (1996). Glossary of terms in quantities and units in clinical chemistry (IUPAC–IFCC recommendations 1996) (ed. H. P. Lehmann, X. Fuentes-Arderiu, and L. F. Bertello). *Pure and Applied Chemistry*, **68**, 957–1000.

A glossary containing terms considered of particular interest to the practising clinical chemist. Definitions taken from a variety of published sources have been provided in a consistent terminology.

22 JCBN (1996). Nomenclature of carbohydrates (recommendations 1996) (ed. A. D. McNaught). *Pure and Applied Chemistry*, **68**, 1919–2008.

An expansion of and replacement for the document entitled 'Tentative rules for carbohydrate nomenclature – part 1, 1969' (reprinted in item 4 at pp. 127–148). It also replaces in essence several other sets of recommendations (also reprinted in item 4) covering various specialized areas of carbohydrate terminology.

URL: `http://www.chem.qmw.ac.uk/iupac/2carb/`

23 IUPAC (1996). Basic terminology of stereochemistry (IUPAC recommendations 1996) (ed. G. P. Moss). *Pure and Applied Chemistry*, **68**, 2193–2222.

A glossary of the more important, and most widely used, stereochemical terms. It extends the list of those defined in Section E (stereochemistry) of item 1 (reprinted in item 4 at pp. 1–18), and includes some terms from inorganic, macromolecular, and physical organic chemistry, as well as some misleading terms (with guidance on correct usage or acceptable alternatives). Mention is made of many of the symbols used in stereochemical nomenclature.

URL: `http://www.chem.qmw.ac.uk/iupac/stereo/`

24 IUPAC (1996). Glossary of terms used in photochemistry (IUPAC recommendations 1996) (ed. J. W. Verhoeven). *Pure and Applied Chemistry*, **68**, 2223–2286.

A revised and enhanced version of a glossary first published in 1988.

25 Clark, B. F. C. and 13 others (1996) Prokaryotic and eukaryotic translation factors — ad hoc nomenclature subcommittee report. *Biochemie*, **78**, 1119–1122.

Proposals for updating and extending to prokaryotic factors the document entitled 'Nomenclature of initiation, elongation and termination factors for translation in eukaryotes — recommendations 1988' (reprinted in item 4 at pp. 90–92). NC–IUBMB has not formally adopted the report (although published under the name of IUBMB), but it has recommended (in item 30) that the proposals should be followed.

26 JCBN (1997). Nomenclature of glycolipids (recommendations 1997) (ed. M. A. Chester). *Pure and Applied Chemistry*, **69**, 2475–2487.

A replacement for the section on glycolipids of the document entitled 'The nomenclature of lipids — recommendations 1976' (reprinted in item 4 at pp. 180–190).

URL: `http://www.chem.qmw.ac.uk/iupac/misc/glylp.html`

27 IUPAC, IUBMB, and IUPAB (1998). Recommendations for the presentation of NMR structures of proteins and nucleic acids (recommendations 1998) (ed. J. L. Markley, A. Bax, Y. Arata, C. W. Hilbers, R. Kaptein, B. D. Sykes, P. E. Wright, and K. Wüthrich). *Pure and Applied Chemistry*, **70**, 117–142. Correction: *ibidem*, 1998, **70**, Errata pp. (or part 6, i).

28 IUPAC (1998). Glossary of terms used in medical chemistry (IUPAC recommendations 1998) (ed. C. G. Wermuth, C. R. Ganellin, P. Lindberg, and L. A. Mitscher). *Pure and Applied Chemistry*, **70**, 1129–1143.

A glossary compiled from a number of sources with the aim of establishing international definition standards in a subject where rapid changes are occurring. Concise definitions in a consistent terminology are provided for about 100 commonly used terms.

URL: `http://www.chem.qmw.ac.uk/iupac/medchem/`

Newsletters

The biochemical nomenclature committees (JCBN and NC–IUB or NC–IUBMB) have together published newsletters in various journals of biochemistry from time to time since 1980. These are designed to inform scientists about the work of the committees, to call attention to features of recommendations that are recently published or are in press, to report on current nomenclature problems under study, and to make recommendations not meriting publication as separate documents.

A schedule of all the published newsletters is included in the publication list available via the World Wide Web and noted at item 33; this schedule enumerates all the appearances in print of each of the newsletters (or of excerpts therefrom) and states their partial contents, with links to the websites of any directly accessible relevant recommendations. The two most recent newsletters are listed below; WWW versions of

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their full texts are available. Excerpts from previous newsletters are included in item 4.

29 JCBN and NC–IUBMB (1997). Newsletter 1996. *European Journal of Biochemistry*, **247**, 733–739; and elsewhere.

Topics covered include: vitamin A, retinoids, and retinoate analogues; absorbance and attenuance; glycosaminoglycans and proteoglycans; biochemical equations, catalytic antibodies; nomenclature of proteins and of receptors; and terminology in immunology. *See also* items 35 and 36.

URL: http://www.chem.qmw.ac.uk/iupac/newsletter/1996/

30 JCBN and NC–IUBMB (1999). Newsletter 1999. *European Journal of Biochemistry*, **264**, 607–609 and elsewhere.

Topics covered include: symbols for selenocysteine; IUBMB–Nicholson metabolic maps; nomenclature recommendations on the World Wide Web; databases for ribosomal proteins and for gene families; and the recommendation regarding translation factors noted under item 25.

URL: http://www.chem.qmw.ac.uk/iupac/newsletter/1999/

Listings

31 Lists of separately published current recommendations on specific topics of biochemical interest issued by JCBN, NC–IUB, NC–IUBMB, or certain other international committees are included in the information or instructions provided to authors by a number of journals of biochemistry (e.g. *Archives of Biochemistry and Biophysics*, *Biochemical Journal*, *European Journal of Biochemistry*, *Journal of Biological Chemistry*) and presented from time to time in the first volume or part of their printed versions issued for a calendar year or posted on their websites. *See also* item 33.

32 A list of all JCBN, NC–IUB, and NC–IUBMB recommendations currently accessible through the World Wide Web, with their URLs and links to WWW versions of their full texts, is provided at the Biochemical Nomenclature Committees home page, together with general information concerning the committees. Included may be newly approved recommendations in advance of the printed versions.

URL: http://www.chem.qmw.ac.uk/iubmb/nomenclature/
or http://www.chem.qmw.ac.uk/iupac/jcbn/

Similar information is presented in item 30

33 A complete list of all JCBN, NC–IUB, and NC–IUBMB publications, enumerating all their appearances in print and including any in translation, is available via the World Wide Web, with links to the websites of those documents directly accessible.

URL: http://www.chem.qmw.ac.uk/iubmb/bibliog/jcbn.html

34 A list of current IUPAC publications on nomenclature and symbolism is included in the instructions to authors provided in the first part issued for a calendar year of certain of the journals published by the Royal Society of Chemistry. The 1999 list includes the main contents of item 4, the section or chapter headings for items 1, 2, 3, and 9, and a subject-by-subject catalogue, complete to mid-1998, of separately published current recommendations on specific chemical topics.

URL: http://www.rsc.org/is/journals/authrefs/jappdx.htm

35 A list of approved documents on the nomenclature of immunology is included in item 29 at p. 737.

36 Lists of other nomenclature and reference publications of interest to biochemists are given in item 4 at pp. 341–347 and in item 29 at p. 738.

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Huynguyen Co. LTD. Biotechnology, Trades and Services, 201 Luong Nhu Hoc, Dist 5, HCMC,
Phone/Fax: (84-8) 9509938, 8551478, 8574867 Handphone: 0918190535, email: huynguyen@huynguyenltd.com.

Appendix C

Organizations that are helpful to biochemists and molecular biologists

Much of the information in this Appendix was collated from sources on the World Wide Web (WWW) in December 1996. The information presented here can be checked or updated by reference either to the ICSU home page:

`http://www.icsu.org`

or the site maintained at the University of Waterloo Electronic Library Scholarly Societies Project:

`http://www.lib.uwaterloo.ca/society/`

International unions

The International Council For Science (ICSU) is a non-governmental organization, founded in 1931 to bring together natural scientists in international scientific endeavour. It comprises 94 multidisciplinary National Scientific Members (scientific research councils or science academies) and 23 international, single-discipline Scientific Unions to provide a wide spectrum of scientific expertise enabling members to address major international, interdisciplinary issues which none could handle alone. ICSU also has 30 Scientific Associates.

The International Council for Science
51 Boulevard de Montmorency
F-75016 Paris
France

Telephone: +33 1 45 25 03 29
Telefax: +33 1 42 88 94 31
E-mail: `secretariat@icsu.org`
WWW URL: `http://www.icsu.org`

The unions concerned with biochemistry and molecular biology which are members of ICSU are:

International Union of Biochemistry and Molecular Biology (IUBMB)
The IUBMB unites biochemists and molecular biologists in 63 countries which are members of the Union. Each country has either an Adhering Body or Associate Adhering Body in the Union which is represented as a biochemical society, as a national research council or as an academy of sciences.

You may reach the IUBMB and learn more about the activities by contacting your Adhering Body or the General Secretary:

Dr Frank Vella
Department of Biochemistry
University of Saskatchewan
18 Leyden Crescent
Saskatoon
Saskatchewan
Canada S7J 2S4

Telephone: +1 306 374 1304
Telefax: +1 306 955 1314
E-mail: `f.vella@sk.sympatico.ca`
WWW URL: `http://www.iubmb.unibe.ch`

International Union of Pure and Applied Biophysics (IUPAB)
The International Union for Pure and Applied Biophysics is a member of the International Council of Scientific Unions family. Affiliated to it are the national adhering bodies of 45 countries. Its function is to support research and teaching in biophysics. The Secretary General, to whom enquiries should be addressed, is:

Professor A. C. T. North
Department of Biochemistry and Molecular Biology
The University of Leeds
Leeds LS2 9JT
United Kingdom

Telephone: +44 113 233 3023
FAX: +44 113 233 3167
E-mail: `a.c.t.north@leeds.ac.uk`
WWW URL: `http://bmbsgi11.leeds.ac.uk/iupab/`

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Phone/Fax: (84-8) 9509938, 8551478, 8574867 Handphone: 0918190535, email: huynguyen@huynguyenltd.com.

Appendix C

International Union of Pure and Applied Chemistry (IUPAC)
Founded in 1919, the International Union of Pure and Applied Chemistry (IUPAC) is a voluntary, non-governmental, non-profit association of National Adhering Organizations representing the chemists, from both industry and academia, of 40 countries. In addition, IUPAC has links with 14 Observer Countries, 30 regional and international Associated Organizations, which are concerned with chemistry and its application, and approximately 160 Company Associates from 24 countries.

IUPAC Secretariat
PO Box 13757
Research Triangle Park
NC 27709-3757
USA

It is geographically located at 104 T. W. Alexander Drive, Building 19, Research Triangle Park, North Carolina

Telephone: +1 919 485 8700
Telefax: +1 919 485 8706
E-mail: secretariat@iupac.org
WWW URL: http://www.iupac.org

International Union of Biological Sciences (IUBS)
The International Union of Biological Sciences (IUBS) was created in 1919, and held its first General Assembly that same year. Its objectives are: to promote the study of biological sciences, to facilitate and coordinate research and other scientific activities that require international cooperation, to ensure the discussion and dissemination of international conferences, and to assist in the publication of their reports. The Executive Committee of IUBS can be contacted at:

IUBS
51 Boulevard de Montmorency
F-75016 Paris
France
Telephone: +33 1 45 25 00 09
Telefax: +33 1 45 25 20 29
E-mail: iubs@paris7.jussieu.fr
WWW URL: http://www.icsu.org/membership/SUM/iubs.html

International Union of Crystallography (IUCr)
The IUCr is a scientific union adhering to ICSU. Its objectives are to promote international cooperation in crystallography and to contribute to all aspects of crystallography, to promote international publication of crystallographic research, to facilitate standardization of methods, units, nomenclatures and symbols, and to form a focus for the relations of crystallography to other sciences.

The Executive Secretary of the IUCr may be contacted at:

International Union of Crystallography
2 Abbey Square
Chester CH1 2HU
United Kingdom
Telephone: +44 1244 345431
Telefax: +44 1244 344843
E-mail: execsec@iucr.org
WWW URL: http://www.iucr.ac.uk/

International Brain Research Organization (IBRO)
The International Brain Research Organization (IBRO) was founded in 1960 in response to the growing demand from scientists in many countries and different disciplines for the creation of a central organization for the better mobilization and utilization of the world's scientific resources for research on the brain. The general objectives and goals of IBRO are: to foster throughout the world fundamental scientific research contributing to an understanding of the brain, normal and abnormal; to promote international collaboration and worldwide education in brain research; and to work through and with existing organizations to help in reaching their own particular objectives and to solicit their aid in the objectives of IBRO. The Executive Committee can be contacted at:

IBRO
51 Boulevard de Montmorency
F-75016 Paris
France
Telephone: +33 1 46 47 92 92,
Telefax: +33 1 45 20 60 06
E-mail: ibro@pratique.fr
WWW URL: http://www.icsu.org/membership/SUM/IBRO.html

International Union of Immunological Societies (IUIS)
The International Union of Immunological Societies (IUIS) was established in May 1969. Its objectives are to organize international cooperation in immunology and to promote communication between the various branches of immunology and allied subjects encourage within each scientifically independent territory cooperation between the societies that represent the interests of immunology and contribute to the advancement of immunology in all its aspects. The IUIS can be contacted c/o:

Keith James (Secretary General of IUIS)
Department of Surgery
Medical School
University of Edinburgh
Teviot Place
Edinburgh EH8 9AG
United Kingdom
Telephone: +44 131 650 3557
Telefax: +44 131 667 6190
E-mail: kjames@srv2.med.ed.ac.uk
WWW URL: http://www.icsu.org/membership/SUM/iuis.html

International Union of Physiological Sciences (IUPS)
The objectives of IUPS are to encourage the advancement of the physiological sciences, to facilitate the dissemination of knowledge in the field of physiological sciences, to foster and encourage research in the field of physiological sciences, to promote the International Congresses of Physiological Sciences, to promote such other meetings as may be useful for

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Phone/Fax: (84-8) 9509938, 8551478, 8574867 Handphone: 0918190535, email: huynguyen@huynguyenltd.com.

the advancement of the physiological sciences, and to promote such other measures as will contribute to the development of physiological sciences in developing countries. The IUPS Secretary General can be reached at:

LGN, Bâtiment CERVI
Hôpital de la Pitie-Salpetrière
83 Boulevard de l'Hôpital
F-75013 Paris
France

Telephone: +33 1 42 17 75 37
Telefax: +33 1 42 17 75 75
E-mail: suorsoni@infobiogen.fr
WWW URL http://www.nas.edu/iups/

International Union of Microbiological Sciences (IUMS)
The International Union of Microbiological Societies (IUMS) can be contacted c/o:

Dr Marc H. van Regenmortel (Secretary General of IUMS)
IBMC
15 rue Descartes
F-67000 Strasbourg
France

Telephone: +33 3 8841 7022
Telefax: +33 3 8861 0680
WWW URL: http://www.icsu.org/membership/SUM/IUMS.html

International Union of Nutritional Sciences (IUNS)
The objects of the International Union of Nutritional Sciences are to promote international cooperation in the scientific study of nutrition and its application, to encourage research and the exchange of scientific information in the nutritional sciences, by the holding of congresses and conferences, by publication, and by other suitable means, to establish such commissions, committees, and other bodies as may be required in the pursuit of the above, to provide a means of communication with other organizations, and to encourage participation in the activities of the International Council of Scientific Unions, of which the Union is a member, and to develop activity regarded as helpful and appropriate in achieving the objectives of the Union. The IUNS can be contacted c/o:

O. M. Galal, Executive Secretary, IUNS
INUS Secretariat
c/o UCLA School of Public Health
International Health Program
10833 Le Conte Avenue
Box 951772
Los Angeles
CA 90095-1772
United States

Telephone: +1 310 20 69639/68444
Telefax: +1 310 794 1805
E-mail: ogalal@ucla.edu
WWW URL: http://www.icsu.org/membership/SUM/iuns.html

International Union of Pharmacology (IUPHAR)
Founded in 1959 as a section of the International Union of Physiological Sciences, 'The International Union of Pharmacology', IUPHAR, has been independent since 1966. The Union is a voluntary, non-governmental, non-profit association of national organizations presently representing the pharmacologists of 47 member countries and three regional associations. IUPHAR is a member of the International Council of Scientific Unions and participates in the work of its scientific committees. It receives international recognition particularly by the United Nations Educational and Scientific Organization. IUPHAR can be contacted c/o:

Paul M. Vanhoutte, Secretary General, IUPHAR
Vice-President Research
Direction de la Recherche et du Developpement
Institut de Recherches Internationales Servier (IRIS)
6 Place des Plèides
92415 Courbevoie Cedex FRANCE

WWW URL: http://www.icsu.org/membership/SUM/iuphar.html

Federations of biochemists and molecular biologists

In addition to the Unions there are four regional organizations for biochemists.

The Federation of European Biochemical Societies (FEBS) which now has 32 constituent societies.
(For address *see* **The Biochemical Society** below.)

WWW URL: http//www.febs.unibe.ch/

The Pan American Association of Biochemists and Molecular Biologists (PABMB).
(For address *see* **American Society for Biochemistry and Molecular Biology** below.)

Federation of Asian and Oceanian Biochemists and Molecular Biologists (FAOBMB) which now has 18 biochemistry and molecular biology societies associated.
(For address *see* **The Japanese Biochemical Society** below.)

The Federation of African Societies of Biochemistry and Molecular Biology (FASBMB)
The Chairman
Department of Biochemistry
University of Nairobi
PO Box 30197
Nairobi
Kenya

International Federation of Clinical Chemists (IFCC) which is loosely linked to IUPAC.

Human Genome Organisation (HUGO)
One Park Square West
London NW1 4LJ
United Kingdom

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Appendix C

Other Regional Organizations

The European Molecular Biology Organization
Postfach 1022.40
Meyerhofstrasse 1
69117 Heidelberg
Germany

European Federation of Biotechnology
For information contact one of the following:

Society of Chemical Industry
14 Belgrave Square
London SW1X 8PS
United Kingdom

DECHEMA
Theodor-Heuss-Allee 25
D-6000
Frankfurt am Main 97
Germany

Societé de Chimie Industrielle
28 rue St-Dominique
F-75007 Paris
France

National Societies

Some of the larger national Biochemical Societies may be noted as follows;

American Society for Biochemistry and Molecular Biology
9650 Rockville Pike
Bethesda
MD 20814
USA

E-mail: kmirabal@faseb.org

The Biochemical Society
59 Portland Place
London W1N 3AJ
United Kingdom

E-mail: genadmin@biochemistry.org.

The Japanese Biochemical Society
Ishikawa Building-3f
25-16, Hongo 5-Chome
Bunkyo-ku
Tokyo
Japan

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Phone/Fax: (84-8) 9509938, 8551478, 8574867 Handphone: 0918190535, email: huynguyen@huynguyenltd.com.

Appendix D

The Internet

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Introduction

This appendix is in three sections: first we present a glossary of terms commonly used in discussions of the Internet; secondly we consider a worked example of how to find a biochemical fact using the Internet's search facilities; finally there is a list of biochemically interesting and/or useful sites. The reader is strongly advised to become familiar with the Internet and to note that it is expanding very rapidly: we do not guarantee that all the sites will remain available for the currency of this Dictionary. Additionally more sites will undoubtedly go on line and the reader should rely on search engines rather than the specific sites that are mentioned here.

Glossary

Some of this glossary is based on N. A. Maughan and J. H. Parish (1995). The Information Superhighway and Biochemistry. *Biochemical Education* **23**, 184–189, © 1995 International Union of Biochemistry and Molecular Biology. Parts of the text are reproduced here with permission.

anonymous FTP FTP access to a site where files, etc., can be accessed.The login name for such a site is 'anonymous' (or 'ftp') and the required password is the user's e-mail address.

applet a little application; this term is used to describe a module written, usually, in Java.

Archie a database listing filenames of files in FTP servers throughout the world. It can be used to locate a particular public domain file if the exact filename is known.

archive *see* **software archive**.

archive format one of a variety of file types in which collections of computer files are put together for storage and retrieval. One of the most common is TAR (tape archive, so called because it was originally designed for this); other examples include *BOO* and *ZOO* files (for PCs); certain other archive formats are **compressed files**.

ASCII *abbr. for* American Standard Code for Information Interchange; a standard set of characters readable by all computers.

bionet names of newsgroups of interest to biochemists start with the text 'bionet'; examples include the newsgroups bionet.plants and bionet.molbio.yeast. *Distinguish from* **BioNet**.

BioNet an educational software consortium whose URL is `http://www.leeds.ac.uk/bionet.html`. *Distinguish from* **bionet**.

bookmark a URL stored in a browser file, usually to allow quick access to a frequently used WWW site without the need to type in the URL.

browser a piece of local software that allows access to WWW pages; an example is **Netscape**.

cgi *abbr. for* Common Gateway Interface: a programming language similar to C used for producing programs, etc., in HTML.

compressed file a computer file (or a collection of these in **archive format**) that has been compressed by an appropriate algorithm, such as that of Lempel-Zif. In UNIX, such files are indicated by the extensions .Z, .gz, or .sh. For PCs they are usually indicated by the extension .zip. Certain compressed files may be programs that compress themselves. Others require a decompression utility such as uncompress, gunzipe (UNIX), and PKUNZIP and WINZIP (PCs). A good **software archive** will include notes (typically in a file called README or 00README) on decompression utilities that are required and copies of any decompression software required for compressed files in their own archive.

DNS *abbr. for* Domain Name Server: a computer, transparent to the average end-user, that parses IP addresses and establishes the necessary connection between the appropriate nodes.

domain part of an **IP address**; in the example given in that entry, '`leeds.ac.uk`' is a domain.

e-mail *abbr. for* electronic mail.

e-mail address an address for e-mail of the form <name>@<address>where the <address> is an **IP address** in its named format, e.g. `howard@bmbus1.leeds.ac.uk` or `j.h.parish@leeds.ac.uk`. Another example is `president@white-house.gov`. Note that e-mail addresses and IP addresses are case-insensitive.

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ethernet low-level protocols and associated hardware (cabling) for computer communications.

ethernet address *an alternative name for* **machine address.**

FTP *abbr. for* file transfer protocol: similar to **Telnet** in that it requires a user name and password but is only capable of transferring files. FTP has limited help facilities (obtained by typing in ?): it uses UNIX conventions for changing directories etc. The most important consideration is to tell the FTP program whether the file transfer is to be binary or ASCII (i.e. text).

Gopher a menu-based alternative to using WWW for finding out what sites contain files you might wish to receive.

home page **1** the first page loaded by a WWW browser such as Netscape when it starts up. **2** the main WWW site for a particular person or group, often a contents list with **links** to connected sites.

http *abbr. for* HyperText transfer protocol; also used as a suffix for computer files that are written in HTML etc.

HTML *abbr. for* HyperText Mark-up Language: an interpreted computer language used for producing HyperText.

HyperText a form of marked text used for certain computer applications.

Internet a large global network of computers that arose from a United States military network (ARPANET) that started in 1969. ARPANET was built to be reliable in that if one part of the network was damaged by enemy action, messages between computers would automatically be re-routed. The in-built reliability between sites makes this type of network popular with all users: any computer on the Internet has the capacity to communicate with any other computer on the Internet. The methods and protocols for communicating on the Internet were finalized in 1985 and programs that use the Internet continue to be developed.

IP *abbr. for* Internet protocol (*see* **protocol**).

IP address a unique address for an Internet computer. It is a software address: although actually a binary number it is usually represented in 'dotted decimal' notation, e.g. 129.11.110.24. Associated with this (for the vast majority of sites) is a 'named' version of this, in the case cited above it is `bmbus1.leeds.ac.uk`. The conventions for such named addresses are fairly straightforward. The last two letters (`uk` in that case) indicate the country: other examples include `ca` (Canada), `in` (India), `de` (Germany), and `si` (Slovenia). The exception is the USA: as IP is American, the default is the USA. The '`.ac`' in the case above means 'academic'; in the UK this field can also be `.gov` (government), `.co` (or, rarely, `.com`; commercial), or `.org` (organization). A similar covention is used in many countries, e.g. in the USA, `.gov` (government), `.com` (commercial), `.edu` (education), `.mil` (military). Some countries (e.g. Germany) do not usually have this field at all.

Java an object-oriented computer language designed for producing WWW pages etc. At the time of writing this glossary, Java is not universally used for this purpose as it has to be interpreted in software and is relatively slow. However, the importance of Java is set to increase as specialized processors designed for running Java programs become available and common. Unlike many computer neologisms, Java is not an acronym but rather a reference to Java coffee, which is popular with the original authors of the language.

link a connection between one WWW site and another; the presence of a link is indicated by underlined and/or coloured text; clicking on this text automatically instructs the browser to open the relevant WWW page.

machine address *or* **ethernet address** a binary number unique to a computer (more exactly its network hardware) that is used by DNS, etc. It should be transparent to the average end-user. The number is usually represented as colon-delimited hexadecimal numbers, e.g. the hardware associated with `bmbus1.leeds.ac.uk` (*see* **IP address**) has the machine address 00:00:f8:20:5f:3a.

Netscape a popular (and highly effective) **browser** available for a variety of personal computers, workstations, and graphics terminals.

newsgroup an electronic bulletin board on the Internet, where anyone can post a message. These messages can be read by anyone else with access to the Internet and readers can post replies to messages. The distinction between electronic mail and newsgroups is that the former is a method of sending private messages to individuals whereas the latter is a means of posting messages in a public arena. Newsgroups therefore provide a flexible and convenient method for exchanging ideas and opinions and getting answers to technical queries. Newsgroups are arranged by subject and the number of newsgroups currently on the Internet is in the thousands. There are several newsgroups devoted to various aspects of biochemistry and therefore some care must be taken to post queries to the most appropriate newsgroup.

news reader a program to read and reply to **newsgroup** messages. Most multi-user systems will have a news reader installed on them. Several news readers are available for PCs and Macintosh machines.

node a point in a computer network where different communication lines connect; it may be a computer or a simpler electronic device, depending on the size and complexity of the network.

protocol a set of rules governing the way that data are exchanged between computers, for example, determining the format of messages.

search engines Internet sites that have facilities for searching for text. Depending on the way in which they work they are variously referred to as Web crawlers, robots, etc. Three good examples are:

```
http://www.yahoo.com
http://www.altavista.com
http://www.search.com
```

software archive a site usually accessed by anonymous FTP, from which public-domain software can be downloaded. Some of the software is binary, i.e. is designed to be loaded directly into a local computer; some is code written in a high-level language (such as C or C++) and needs to be compiled locally. Typically software for PCs (Windows or Windows95) and Macintosh computers is of the former type and more generic code and software for UNIX systems is of the latter.

SRS *abbr. for* Sequence Retrieval System: a system for molecular biologists that contains links to the major sequence and 3-D structure databases etc. Examples are listed under 'Molecular biology research tools' below.

system adminstrator a person you should get in touch with if you are setting up an internet node for the first time.

Telnet a method of logging into a computer on the Internet from another Internet computer (which could be in the same room or across the world). Telnet is typically used to access remote computers which have facilities on them not available locally. For example, a researcher may want to query a library catalogue or access a database containing information on protein sequences.

URL *abbr. for* uniform resource locator: a method for identifying WWW sites, which is 'uniform', i.e. independent of any specific protocol. URLs have a characteristic convention of starting `<type>://address`. FTP and Gopher sites start '`ftp://`' and '`gopher://`' respectively. WWW sites start '`http://`'. Here is a fairly typical URL:

```
http://www.leeds.ac.uk/
```

Note that the `www.` field is optional and is not found at all sites. The URL can be extended by adding a level down and/or an actual page reference as, following that example,

```
http://www.leeds.ac.uk/bmb/bmb.html
```

In that example 'bmb' is the name of a Department (Biochemistry and Molecular Biology) and '`bmb.html`' is an example of a **home page**.

uniform resource locator *see* URL.

Usenet collectively, the **newsgroups** on the Internet.

WAIS *abbr. for* wide area information system: a system for the retrieval of documents etc. that supports a directory of servers and is useful for certain free text searches.

W3 *abbr. for* World Wide Web (*see* **WWW**).

World Wide Web *see* **WWW**.

WWW *or* **W3** *abbr. for* World Wide Web; a network of pages on the Internet. The pages combine formatted text and graphics. The characteristic feature of the WWW is the way in which the pages are cross-referenced using **links**. The pages are distributed: they can be on local machines or in another country.

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Phone/Fax: (84-8) 9509938, 8551478, 8574867 Handphone: 0918190535, email: huynguyen@huynguyenltd.com.

Getting started

The list of URLs given below may seem somewhat daunting. A useful first step in getting acquainted with the Internet is to carry out a MEDLINE search. To do this, follow the steps below.

1. Using your browser, type in the URL, `http://www3.ncbi.nlm.nih.gov/Entrez/` (NOTE: the capital E of Entrez is important). This will take you to a very valuable US government site that offers a range of information.
2. In the list of databases, under 'Search WWW Entrez', click on Search the molecular biology subset of MEDLINE. A screen appears in which there is a white box which invites you to 'Enter Term'. Place your cursor in this box, and type in a term for which you would like references. For example you could type in 'citrate synthase'. Then click on the grey box that says 'Accept'. If you do this, a screen appears that contains a grey box telling you that (at the time of writing) there are 620 documents. In fact it says 'Retrieve 620 documents'.
3. Below it there is a smaller white box that allows you to limit the number of documents to be passed to you. The default on this is 50 documents – you can alter it as you wish, but remember that transfer of a large number of documents may take a very long time.
4. When you have decided how many of the documents you wish to transfer, click on 'Retrieve 620 documents' (the number in the grey box remains the same, but only 50, or such number as you have typed in the white box, will be transferred).
5. A list of citations, starting with the most recent, appears on the screen. Below each citation, a list of options will be found. One of the most useful of these is Abstract format. If you click on this, an abstract of the document (available in most, but not all cases) will appear.

URLs of use in biochemistry

Users are advised that pages are subject to change without notice. If you are unable to find a particular page try altering the search criteria.

Search engines (general)

`http://www.yahoo.com/`
A comprehensive search engine that is easy to use but requires some guessing as to what categories should be searched. Other search engines can be accessed via Yahoo.

`http://www.altavista.com/`
A comprehensive search engine that is a good starting point if you do not know what subcategory to start with but which produces large numbers of URLs if the key word(s) are not specified carefully. Its Advanced Search option allows the use of Boolean operators such as AND and OR and the user can dictate the date of the items searched and the order in which the search results are displayed.

`http://http.demon.net/external/cusi.html`
Similar to Yahoo, worth using in Europe in the afternoon when North American Internet activity can slow down transatlantic access to Yahoo.

`http://www.lycos.com/`
A popular if idiosyncratic browser for the WWW; not always suitable for scientific enquiries.

`http://www.search.com/`
A set of links to AltaVista and Magellan (a comparable site); it also provides direct search facilities of its own.

`http://netscape.com/home/internet-search.html`
The URL that is accessed if Netscape users choose 'Net Search' from their Netscape window. It allows searching and provides access to AltaVista, Magellan, Yahoo, Lycos, etc.

`http://www.wais.com/`
A starting point for WAIS servers.

Molecular biology and bioinformatics search engines

A very useful starting point is Pedro's list: it is available in copied (mirrored) sites in several continents as follows:

USA: `http://www.public.iastate.edu/~pedro/research_tools.html`
Europe: `http://www.biophys.uni-duesseldorf.de/bionet/research_tools.html`
`http://www.fmi.ch/biology/research_tools.html`
Asia: `http://www.peri.co.jp/Pedro/research_tools.html`

Pedro's list provides links to databases, software and analysis tools and is incorporated into a search engine at `http://www.ebi.ac.uk/htbin/bwurld.pl`

Some other useful general starting points:

`http://www.molbiol.ox.ac.uk`
`http://info.er.usgs.gov/network/science/biology/index.html`
`http://www.bioinf.leeds.ac.uk/bioinformatics.html`
`http://www.hgmp.mrc.ac.uk/Bioinformatics`
`http://www.bio.cam.ac.uk`
`http://www.abc.hu/biosites.html`
`http://golgi.harvard.edu/biopages.html`
`http://www.ebi.ac.uk/general/other_bioservers.html`
`http://rldb.rz_berlin.mpg.de./links/biolinks.html`

Maps and models

Several sites that are excellent for teaching (including self-education):

`http://www.genome.ad.jp/`
(this is also a very extensive site for genome links)
`http://www.imb-jena.de/IMAGE.html`
(for 3-D structures)
`http://www.biochemgen.ucsd.edu/`
(human metabolic disorders)
`http://www2.shef.ac.uk/chemistry/web-elements/web-elements-home.html`

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Appendix D

(periodic table of chemical elements)
`http://cst.lanl.gov/julie/imagemap/periodic.periodic.html`
(rather more colourful and detailed version)

Genome projects

Entries with the prefix 'bionet.' are news groups.

Arabidopsis
`bionet.genome.arabidopsis`
`http://weeds.hgh.harvard.edu/`

Caenorhabditis elegans
`bionet.software.acedb`
`bionet.software.gcg`
`http://moulon.inra.fr/acedb/acedb.html`

Drosophila melanogaster
`bionet.drosophila`
`gopher://bio.net/11/DROS/`
Flybase (many mirror sites available)
`http://morgan.harvard.edu/`

Escherichia coli genome project
`http://www.genetics.wisc.edu/`
`http://www.ai.sri.com/ecocyc/ecocyc.html`
links metabolic maps to genes etc.

Human Genome Project: several starting points include
`http://shgc.stanford.edu/`
`http://mendel.hgp.med.umich.edu/`

Mouse
`http://glengoyne.hgu.mrc.ac.uk/`
`http://mickey.utmem.edu/`

Xenopus
`gopher://gopher.bio.net/11/URODELES`

Yeast
`bionet.molbiol.yeast`
`http://genome-www.stanford.edu/`

Zebrafish
`bionet.organisms.zebrafish`
`http://zebra.scarolina.edu/`

Databases

Ribosomal database project for taxonomy based on rRNA
`http://rdb.life.uiuc.edu/`

Protein and nucleic-acid sequence/structure databases
`http://www.ncbi.nlm.nih.gov/` (GenBank etc.)
`http://www.nih.gov/molbio/`
`http://www.dl.ac.uk/SEQNET/home.html`
`http://www.boklabs.wisc.edu/seq.html`
(mainly viral sequences etc.)
`http://pdb.pdb.bnl.gov/`
(Brookhaven structural database)

REBASE (restriction enzymes)
`http://www.gdb.org/Dan/rebase/rebase.html`

SCOP (a structural classification of proteins)
`http://www.bio.cam.ac.uk/scop/`

Molecular biology research tools

Software to run remotely

For access to software involved in protein and nucleic-acid sequence analysis including structure prediction and relationship of 'your' sequence(s) to known sequences, the number of sites is vast. The best starting point is an SRS server: choose one from the following:

Australia	`http://wehiz.wehi.edu.au/srs/srsc`
Belgium	`http://ben.vub.ac.be/srs/srsc`
Eire	`http://acer.gen.tcd.ie/srs/srsc`
Finland	`http://cypress.csc.fi:8001/srs/srsc`
France	`http://www.infobiogen.fr:80/srs/srsc`
Germany	`http://www.embl-heidelberg.de/srs/srsc`
Hungary	`http://hubi.abc.hu/srs/srsc`
Israel	`http://dapsas.weizmann.ac.il/srs/srsc`
Japan	`http://srs.dna.affrc.go.jp/srs/srsc`
Netherlands	`http://www-srs.caos.kun.nl/srs/srsc`
Norway	`http://bioslave.uio.no:8001/srs/srsc`
Sweden	`http://wwwd.bmc.uu.se:80/srs/srsc`
UK	`http://www.ebi.ac.uk/srs/srsc`
	`http://www.sanger.ac.uk/srs/srsc`
	`http://srs.hgmp.mrc.ac.uk/srs/srsc`
	`http://www.seqnet.dl.ac.uk/srs/srsc`
USA	`http://www.ch.embnet.org/srs/srsc`
	`http://www.at.embnet.org/srs/srsc`
	`http://iubio.bio.indiana.edu:81/srs/srsc`
	`http://mcbi-34.med.nyu.edu/srs/srsc`

A good general-purpose European site (with links) for molecular biology applications is the Java Molecular Biology WorkBench
`http://www.embl-heidelberg.de/~toldo/JaMBW.html`

Three useful starting points for commonly used services and links are as follows:

1. mowse: given fragmentation patterns with protein-cleavage reagents and peptide mass fingerprints, mowse will guess the protein(s) that correspond to the data.
   `http://www.hgmp.mrc.ac.uk/Registered/Webapp/mowse/`
2. The Leeds Bioinformatics Project: a convenient collection of alignment and other software that all runs from the same site.
   `http://bmbsgi11.leeds.ac.uk/`

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3. BLAST (Basic Local Alignment Search Tool): a fast method for finding locally optimized sequence alignment; it is popular for identifying given sequences in a database. The most recent implementation of BLAST is Ψ-BLAST and the service is at
   `http://www.ncbi.nlm.nih.gov/cgi-bin/BLAST/nph-psiblast`

Sources of public-domain software

A convenient and easily used starting point:

`gopher://gopher.molbiol.ox.ac.uk:70/1`

Convenient software archive for molecular biology (and some other topics)

`ftp://ftp.EMBL-heidelberg.de`

`ftp://ftp.ebi.ac.uk`

Large general sites and databases

`ftp://ncbi.nih.gov`
A very large archive of molecular biology and mathematics programs

`ftp://unix.hensa.ac.uk`
and
`ftp://micros.hensa.ac.uk`
UK national public-domain software archive (not specifically molecular biology)

`ftp://ftp.gdb.org/`
GDB and OMIM FTP repository (human genome and genetic traits)

`ftp://golgi.harvard.edu/pub/`
GDE (Genetic Data Environment) (Harvard)

`ftp://ftp.bchs.uh.edu/pub/gene-server/`
Gene-server: software and PIR (Houston)

`ftp://turbo.bio.net/pub/`
Intelligenetics

`ftp://ftp.gdbnet.ad.jp/pub/`
Japan Information Center of Science and Technology; biological databases and software mirror for the Pacific area

`ftp://ncbi.nlm.nih.gov/repository/`
NCBI Repository FTP archive

`gopher://fly.bio.indiana.edu:70/11/IUBio-Software%2bData`
IUBio-Software+Data (Indiana)

`ftp://ftp.tigr.org/estdb/`
expressed sequence tag database (TIGR)

`ftp://encyclo.jax.org/pub/`
Encylopedia of the mouse genome (Jackson Laboratory)

`ftp://pdb.pdb.bnl.gov/`
PDB 3-D coordinates of proteins (Brookhaven)

`ftp://vent.neb.com/pub/`
REBASE restriction enzyme database (NEB)

`gopher://weeds.mgh.harvard.edu:70/11/arabidopsis/aatdb`
AAtDB FTP archive

`gopher://s-crim1.daresbury.ac.uk:70/11/EMBnet%20Bioinformation%20Resource%20UK/Data%20%26%20Software/databases`
Assorted databases from SERC Daresbury UK

`gopher://rdpgopher.life.uiuc.edu:70/1/`
Ribosomal Database Project (UIUC)

`gopher://ndb.rutgers.edu:70/11/etc/ndb_link_files`
Nucleic Acid Database (NDB) archive

Molecular graphics

`ftp://nemo.life.uiuc.edu/pub/`
3-D protein display and sequence analysis for the PC (UIUC)

`ftp://brise.imag.fr/pub/mac/programs/`
FoldIt (light) molecular graphics (Macintosh)

`ftp://orion.oac.uci.edu/protein/`
Kinemages, Mage, Pkin: 3-D protein display for the Macintosh and PC (UIC)

`ftp://iqm.unicamp.br/pub/chemistry/`
molecular graphics, dynamics and chemistry (Brazil)

`ftp://ion.rice.edu/pub/`
MolViewer: molecule-viewing program for NeXT (Rice)

`ftp://ftp.dcs.ed.ac.uk/home/ftp/pub/rasmol/`
RasMol: molecular graphics visualization tool for UNIX and PC (UK)

`ftp://sprite.Berkeley.edu/tkrasmol.tar.Z`
RasMol: extended interface (Berkeley)

`ftp://cuhhca.hhmi.columbia.edu/pub/programs/`
PDBview: view 3-D protein structures (Columbia University)

`ftp://stanzi.bchem.washington.edu/pub/raster3d/`
Raster3D: molecular graphics package

`ftp://ftp.msc.edu/pub/xmol/`
XMol: display and analysis of molecular model data (MSC)

Sequence and structure alignment and comparison

`ftp://ibcp.fr/pub/`
ANTHEPROT: protein sequence and 3-D structure analysis (France)

`ftp://ftp.cs.unc.edu/pub/bioscan/`
BioSCAN: biopolymer similarity analysis (UNC)

`ftp://cmgm.stanford.edu/pub/IGdb/`
BLAST and FASTA scripts (Stanford)

`ftp://ftp.ncifcrf.gov/pub/delila/`
DELILA: sequence analysis system (NCI/FCRDC)

`ftp://virginia.edu/pub/fasta/`
FASTA database search program (Virginia)

`ftp://groucho.cs.psu.edu/`
LAV, LAD, Band, & TNB: sequence alignment and analysis (PSU)

`ftp://gnomic.stanford.edu/pub/`
SAPS: statistical analysis of protein sequences (Stanford)

`ftp://ftp.cc.umanitoba.ca/psgendb/`
XYLEM & FSAP: molecular database and analysis packages (Manitoba)

`gopher://sio.ucsd.edu:70/11/SIO-Departmental%20Gophers/MBRD/haygood`
spreadsheet macros for colouring sequence alignments

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Appendix D

Experimental molecular biology utilities

`ftp://ccp4.dl.ac.uk/pub/ccp4/`
CCP4: programs for protein crystallography (UK)

`ftp://ftp.cs.yale.edu/pub/double_digester/`
double digester for restriction enzymes (Yale)

`ftp://peipa.essex.ac.uk/ipa/src/process/`
LaboImage: image processing and analysis (including 1-D gel analysis)

`ftp://zippy.nimh.nih.gov/pub/nih-image/`
NIH Image: image processing and analysis

Molecular modelling and prediction

`ftp://ftp.scripps.edu/pub/`
FLEX 3D (The Scripps Institute)

`ftp://ftp.tigr.org/pub/`
Gene Modeller, ADE (TIGR)

`ftp://ftp.biochem.ucl.ac.uk/pub/MEMSAT/`
MEMSAT: membrane protein structure and topology

`ftp://mbcrr.harvard.edu/MBCRR-Package/`
MBCRR programs (Harvard)

`ftp://crocus.medicine.rochester.edu/jones/`
MOBOSOL: MOPAC modified for AMSOL and NBO (Rochester)

`ftp://sheep0.chem.uic.edu/dist/`
MOIL: molecular dynamics (UIC)

`ftp://ouchem.chem.oakland.edu/pub/`
MOPAC60, AMPAC2.1, and MOPAC50ESP (Oakland)

`ftp://ns.niehs.nih.gov/`
MULTI: molecular modelling (NIEHS–NIH)

`ftp://expasy.hcuge.ch/pub/ProMod/`
ProMod: 3-D modelling software (Geneva)

`ftp://bsmcha1.biochem.ucl.ac.uk/pub/hbplus/home.html`
HBPLUS: hydrogen bond calculator

`ftp://nrcbsa.bio.nrc.ca/pub/`
RNA secondary structure software (NRC, Canada)

`ftp://ftp.itc.univie.ac.at/pub/RNA/`
ViennaRNA: fold and compare RNA secondary structures (Vienna)

Taxonomy, genomes, and genetics

`ftp://spider.ento.csiro.au/delta/`
DELTA: description language for taxonomy (Australia)

`ftp://toolik.stanford.edu/pub/hgmc/`
Human Genome Mapping Center (Stanford)

`ftp://evolution.genetics.washington.edu/pub/`
PHYLIP phylogeny package (Washington)

`ftp://genome.wi.edu/pub/`
Primer, Mapmaker, Mouse SSLP maps (Whitehead)

`ftp://zoo.toronto.edu/pub`
Random: cladistic randomization routines (Toronto)

`ftp://relay.cs.utoronto.ca/pub/molbio/ramha1/`
RAMHA: random mutagenesis simulation (Toronto)

`ftp://genome.stanford.edu/pub/`
Yeast Genome Project (Stanford)

`gopher://megasun.BCH.UMontreal.CA:70/11/CMB/Phylogeny/Treecon`
Treecon: phylogeny, evolutionary trees

`gopher://huh.harvard.edu:70/11/software`
TAXACOM systematic biology (Harvard)

`gopher://megasun.BCH.UMontreal.CA:70/11/CMB/Phylogeny`
Phylogenetic analysis programs, help, etc. (megagopher)

`gopher://larry.pathology.washington.edu:70/1`
chromosome idiograms, human and mouse

`gopher://corona.med.utah.edu:70/11/pub`
linkage and pedigree software and STS probes (Utah)

Miscellaneous

`ftp://ftp.vt.edu/pub/biotechnology/`
National Biological Impact Assessment Program (Ag. Biotech)

`gopher://gopher.gdb.org:70/11/softsearch/.soft-arch-merlot/sas-macros`
SAS macros for the Analysis of Clinical Trial Survey and Energy Survey Data

`gopher://dean.med.uth.tmc.edu:70/11/Biomedical_Shareware/`
Biomedical_Shareware (Texas Medical School)

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Appendix E

Exploring the language of bioinformatics

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http://www.biochem.ucl.ac.uk/bsm/dbbrowser

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Introduction

Ten years from the dawn of the field of bioinformatics, we are beginning to harvest the copious fruits of the various genome projects. In spite of early flood warnings, the resulting torrent of sequence information has all but broken our databanks. The endeavour to cope with, and to rationalize, these vast quantities of data has required cooperation on a global scale. Today, there are hundreds of bio-databanks around the world, many of which are now linked together over the Internet via the World Wide Web (WWW). The WWW is now the vehicle of choice for disseminating biological information, and the resources discussed in the following pages can be pursued further using the Web addresses given in Table 3.

The first step, then, in facilitating access to biological information is to assemble it into central, shareable resources, i.e. databases. There are many different database types, depending on the nature of information being stored and the manner of its storage. For example, two of the themes that dominate bioinformatics research are the acquisition and storage of protein primary and tertiary structures. But the level of complexity involved in archiving a three-dimensional structure is clearly very much higher than that required to store linear amino-acid sequences. Separate disciplines have therefore evolved to manage, or curate, these different database types and to analyse the information they contain. The computational investigation of primary structures (which will henceforth be referred to as sequences) and of tertiary structures (henceforth referred to simply as structures) is known as protein sequence and protein structure analysis respectively (sequence analysis in this context is thus not to be confused with sequence determination).

In the course of this discussion, we will encounter primary,

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secondary, composite, and other, specialist databases. Such resources store different levels of information in completely different formats, leading to a variety of communication problems. However, the advent of user-friendly Web browsers has addressed many of these difficulties, and emerging network technologies are providing exciting new tools with which to brave the information revolution.

The need to harness the sea of biological information is still acute. There are currently more than half a million sequences in public and private databases around the world. This is to be contrasted with the number of known protein structures, now around 5000. This represents a vast information deficit. But, locked up in protein sequences is a huge amount of structural, functional, and evolutionary information. The goal, then, is to try to unearth this information and convert it into biochemical knowledge.

The ultimate challenge, that of predicting protein structure from the linear amino-acid sequence, is unlikely to be realized for decades to come. We do not yet understand enough about the rules that govern protein folding, nor do we have sufficient structures in our databases to make prediction from sequence feasible in the short term. The state of the art, in terms of both sequence and structure analysis, is thus currently at the level of pattern recognition. For protein structures, fold-recognition algorithms (which rely on building reference libraries of protein-fold templates) are only about 50–60% reliable. Such approaches will improve as the database of known structures expands. For protein sequence analysis, the reliability of family/function recognition (which relies on building compendia of protein sequence descriptors) is much higher, but varies considerably with the type of analysis method employed. The difficulty is in being able to distinguish between the mathematical significance of a result returned by a database search algorithm and its biological significance.

The principle of sequence analysis hinges on the observation that sequences belonging to families have accumulated mutations, presumably within an unknown archetype, and that divergent drift is characteristic of the family. Such homologous relationships can be identified with ease where levels of sequence identity remain high, but when these drop to below 50% it becomes increasingly difficult to establish relationships reliably. Analyses can be pursued with decreasing certainty towards the 'Twilight Zone' (the 0–25% identity range), where results are no longer statistically significant. Within the Twilight Zone, alignments may appear plausible to the eye, but cannot be supported by statistical methods. Although sequences may diverge to such an extent that little or no similarity remains at the sequence level, their structures are more likely to be preserved. Such relationships can no longer be detected by sequence-based methods, but fall into the realm of fold recognition.

The following pages aim to provide a guide to the terms used (and abused) in the fields of protein sequence and structure analysis. A list of WWW addresses is given to allow readers to obtain the most up-to-date information about the various databases and resources discussed.

Sequence analysis

Identifying conserved motifs within sequences can provide insights into protein structure and function, and allow us to establish means of classification. The goal is to rationalize the data in the primary sources, by assigning sequences to families. The essence of those families is distilled into potent sequence descriptors that are housed in secondary databases, which then facilitate the diagnosis of future query sequences used to search the database. It is important to establish secondary databases because the primary sources are growing at such a rate that it is becoming increasingly difficult to resolve distant relationships from background noise.

The underlying tool of sequence analysis methods is multiple sequence alignment. Application of those methods involves the derivation of some kind of representation, or abstraction, of conserved alignment elements, which may be diagnostic of structure or function. A bewildering array of terms is used to describe the different types of data representation employed by the various approaches: e.g., motifs, segments, patterns, regular expressions, rules, profiles, signatures, fingerprints, features, domains, and blocks. Several of these have fairly well-defined meanings, but difficulties arise when they are used interchangeably. Some basic definitions of these, and other, concepts are outlined below.

Family, superfamily, clan

It should be relatively straightforward to understand the terms family and superfamily, which usually imply shared functional characteristics and an obvious sequence relationship. Nevertheless, there is still debate regarding when and how properly to use them. The G-protein-coupled receptors (GPCRs) provide a useful illustrative example. The adrenoceptors, muscarinic receptors, opioid receptors, opsins, etc., are distinct protein **families** with characteristic pharmacological and signalling profiles: for example, they may be separated on the basis of the ligands they bind, their tissue distribution, the second-messenger systems to which they couple, or their amino-acid sequences. In most cases, the families may be divided into receptor subtypes, depending on their selectivity for particular agonists and antagonists, which specificities are reflected in slight changes in their primary structures. All of these receptor families share the same structural framework, which is thought to consist of seven transmembrane (7TM) helices. They thus belong to a **superfamily** (which for historical reasons has been termed rhodopsin-like) that is characterized by a unique 7TM signature. This can be readily identified by sequence analysis approaches.

The rhodopsin-like GPCR superfamily, then, can be identified by its characteristic transmembrane sequence signature, and its individual family members resolved from it on the basis of characteristic changes, primarily in the loop regions that lie between the transmembrane helices. At least five other GPCR families are now known, all of which appear to contain 7TM domains, but share no discernible sequence similarity with the rhodopsin-like superfamily. The term **clan** has been coined to describe such a group of families, for which there are indications of an evolutionary relationship, but between which there is no statistically significant similarity of sequence.

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Appen

It is important to define these terms with care, because of the underlying evolutionary implications. The shared sequence similarities within families and superfamilies suggest divergence from a single common ancestor. By contrast, the relationship between clan members is unclear: it may be the result of divergence from a remote ancestor, or it may have arisen through independent convergence to a common function and architecture.

Homology

Protein sequences are said to be homologous if they are related by divergence from a common ancestor. This very simple definition is confounded and abused in the literature. Homology is not a measure of similarity – it is an absolute statement that sequences have a divergent rather than a convergent relationship. Thus phrases that quantify homology (e.g., 'the sequences show 50% homology', or 'sequences are 70% homologous', or 'have a high degree of homology') are, strictly, meaningless and should be avoided.

Motifs

When building a multiple sequence alignment, as more divergent sequences are added, insertions are often required to bring equivalent parts of adjacent sequences into the correct juxtaposition. At the end of such a process, islands of conservation may be observed appearing within a sea of mutational changes, as shown in Figure 1. These conserved regions, which are often quite short (typically 10–20 amino acids in length), tend to denote the structural or functional core of the protein. Their conserved nature allows them to be used to diagnose family membership via a range of sequence analysis techniques. They are most frequently termed **motifs**. Synonymous terms are **block**, **segment**, and **feature**.

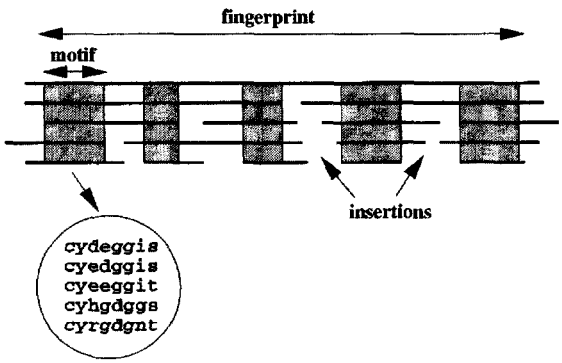

Figure 1. Conserved motifs in a multiple sequence alignment, representing the core structural and key functional sites of the aligned protein family. The broken horizontal parallel bars denote the sequence alignment; the shaded boxes show the locations of the motifs, groups of motifs forming characteristic fingerprints; the excerpt indicates typical residue frequency information contained within a motif, which provides the basis for database searching.

Patterns

For database searching, the sequence data within an individual motif can be reduced to a single **consensus** expression. That expression discards all but the most signficant residue information, concentrating on the most highly conserved positions. The expression shown in Figure 2 tells us that positions 1, 5, 9, and 11 are completely conserved; positions 3, 4, 10, 12, and 13 allow one of two possible residues (whatever is specified within square brackets is allowed at that position); positions 2 and 7 can be anything (X); and position 8 can be anything except proline or glycine (whatever is specified within curly brackets is *not* allowed at that position). Such expressions are used to trawl sequence databases for *identical* matches; their use is relatively limited because they tolerate no similarity. In other words, a sequence that is 99% similar is regarded as a mismatch – thus, for example, a sequence consistent with the expression in Figure 2, but with leucine in place of the allowed isoleucine or valine at position 3, would not be matched, in spite of showing only a single, conservative substitution. The result of searching a database with such an expression is therefore either an exact match, or no match at all; the outcome is either 'on' or 'off', and may hence be referred to as a binary event. Expressions of this type are most frequently termed **patterns**. Synonymous terms are **regular expression** and **signature**.

```
Alignment        Expression

GAVDFIALCDRYF
GPIDFVCFCERFY    G-X-[IV]-[DE]-F-[IVL]-X-{PG}-C-[DE]-R-[FY]2
GRVEFLNRCDRYY
```

Figure 2. Generation of a regular expression from a multiple sequence alignment. The single-letter amino acid code is used: X denotes any residue; square brackets group together the allowed residues at a given position; curly brackets group together the disallowed residues at a position.

Rules

Regular expression patterns are used to greatest diagnostic effect when, within a given sequence alignment, a highly conserved motif (typically 10–20 residues in length) is found to characterize that specific protein family (this might be a core piece of the protein architecture, or it might carry critical functional residues). Often, however, it is possible to identify much shorter, generic patterns within sequence alignments. These tend to be diagnostic of specific functional sites: e.g., sugar attachment sites, phosphorylation, hydroxylation, myristoylation, sulfation sites, etc. These patterns, which are often only three or four residues long, do not provide good discrimination, but can give a guide as to whether a certain type of site *might* exist in a sequence. They are most frequently termed rules. Synonymous terms are **pattern** and **regular expression**.

Fingerprints

Patterns have very limited diagnostic power because they require target sequences to match the expression exactly. Thus, as we have seen, a sequence that fits a pattern at all but one position will be rejected as a mismatch. To address this problem, it is possible to build more powerful discriminators.

Within a sequence alignment, it is usual to find not one, but several motifs that characterize the aligned family (see Figure 1). Diagnostically, it makes sense to use all the conserved regions to build a family signature, so that in a database search there is a higher chance of identifying a distant relative, whether or not all parts of the signature are matched.

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In an approach of this sort, the motifs are treated independently. The sequence information they contain is converted into scoring tables that are populated only by the observed residue frequencies at each motif position. The scoring system is thus considered to be unweighted, in the sense that no additional scores (e.g., from mutation or substitution matrices) are used to enhance discriminating power. However, diagnostic performance is enhanced by iterative database scanning. The motifs therefore grow, and become more mature, with each database pass, as more sequences are matched and added to the scoring tables. Full potency is gained from the mutual context provided by motif neighbours, which allows sequence identification even when some parts of the signature are absent. Thus, for example, a sequence that matches only four of seven motifs may still be diagnosed as a true match if the motifs are matched in the correct order in the sequence, and the distances between them are consistent with that expected of true neighbouring motifs. Groups of aligned, ungapped, unweighted segments of this type are most frequently termed **fingerprints**; they are also called **signatures**.

Blocks

As mentioned above, the constituent motifs of a fingerprint are unweighted (i.e. the scoring system uses only observed residue frequencies), which sometimes leads to relatively poor diagnostic performance. However, it is possible to build more powerful representations of motifs by applying different weighting schemes. In one approach, sequence segments within a motif are clustered to reduce multiple contributions to residue frequencies from groups of closely related sequences. Each cluster is then treated as a single segment, each of which is assigned a score that gives a measure of its relatedness; the most distant segment is given a weight of 100. Most protein families will be defined by several such clustered, weighted motifs. For a given query sequence, as with a fingerprint, the more motifs matched, the greater the confidence that the sequence belongs to that family. Aligned, ungapped, weighted segments of this type are most frequently termed **blocks** (synonymous terms are **motif**, **segment**, and **feature**).

Profiles

By contrast with the use of patterns, blocks, and fingerprints, an alternative approach is to distil the sequence information within *complete* alignments into scoring tables. Such tables define which residues are allowed at given positions, which positions are highly conserved and which degenerate, and which positions, or regions, can tolerate insertions. The scoring system is intricate, and may include evolutionary weights and results from structural studies, as well as data implicit in the alignment. In addition, variable penalties are specified to weight against insertions and deletions occurring in core secondary structure elements. Such tables are used to search databases for similar matches, their inherent complexity rendering them very potent discriminators. They are most frequently termed **profiles**. **Weight matrix** and **position-specific scoring table** are synonymous terms.

Structure analysis

The terms 'domain' and 'module' are not to be confused with the jargon of protein sequence analysis. These terms have specific definitions in the context of protein structure (although they are often used imprecisely and cause confusion). It is beyond the scope of this discussion to consider structure analysis in detail, but in order to draw the distinction from the terms used in sequence analysis, the concepts of domains and modules are outlined below.

Domains

Domains are compact, local, semi-independent folding units that need not be formed from contiguous regions of an amino-acid sequence: they may be discrete entities, joined only by a flexible linking region of polypeptide chain; they may have extensive interfaces, sharing many close contacts, and they may exchange chains with domain neighbours. In the simplest genetic terms, domains may be considered to have arisen via gene fusion and gene duplication events. Multifunctional enzymes, for example, are most readily understood in terms of gene fusion: the dehydrogenases are believed to have arisen from the fusion of a gene coding for a dinucleotide-binding domain with a series of genes, each coding for different catalytic domains. By contrast, the structural domains of chymotrypsin (anti-parallel beta-barrels with identical topology), are thought to have arisen by gene duplication, the interface between the domains providing the catalytic crevice.

In light of the complexity of protein architecture, these examples are somewhat simplistic. The rationalization and classification of protein folds is an arcane discipline, which has led to the development of a variety of domain and fold databases. Currently, amongst the most well-known of these are the scop (Structure Classification Of Proteins) resource, the CATH protein structure classification database, and the ProDom protein domain database. All of these databases are accessible via the WWW, and readers are referred to their Web addresses (see Table 3) for further information.

Modules

Modules are autonomous folding units, and as such can be thought of as a subset of protein domains. They are contiguous in sequence and are frequently used as building blocks to confer a variety of complex functions on the parent protein. In genetic terms, the spread of modules cannot be explained by simple gene duplication and fusion events, but is largely thought to be the result of genetic shuffling mechanisms. It is useful to make a distinction between extracellular modules (e.g. the fibronectin 3, immunoglobulin, and EGF modules) and intracellular modules (e.g. Src homology 2 and 3 (*see* **SH domain**), and pleckstrin homology): their cellular location is seldom interchangeable, and their methods of propagation differ. It is argued that extracellular modules are encoded by exons that are flanked by introns, and that these exons can be shuffled, while being protected by their intron buffers. This model does not hold for bacteria, which have no introns, suggesting that other methods of propagation exist. There is also no observed correlation with intron borders for intracellular modules, suggesting either a different shuffling mechanism, or that intracellular modules arose much earlier. For

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further information, please refer to the WWW address given in Table 3.

Applications of sequence analysis methods: examples

The examples below indicate how functional sites, domains, modules, and families may be encoded by different sequence analysis approaches. (Different methods encode sequence alignment information in different ways – e.g. frequency tables, weight matrices, profiles, etc.) In each case, a regular expression is given (as indicated by the accession number and code retrieved from PROSITE 13.0), and corresponding references to blocks, fingerprints, and profiles are provided where such information exists. The full current lists of patterns, fingerprints, and profiles are available from the WWW addresses given in Table 3.

Functional sites

Functional sites usually contain only two or three key residues, which can be encoded by regular expression rules. Rules are too short to be diagnostically reliable, and can only give a guide as to whether a particular attachment site, glycosylation site, splice site, etc., might be present. A 'hit' with a rule should therefore be supported by biochemical evidence.

N-glycosylation site (PS00001 ASN_GLYCOSYLATION)[8]

N-{P}-[ST]-{P}

Possible *N*-glycosylation sites may be located with the rule shown above. Proline residues are disallowed at positions 2 and 4, as their presence at these points may hinder correct folding of the sequence and inhibit glycosylation. There is no true family, per se, defined by this functional site; consequently, equivalent blocks, profiles and fingerprints have not been derived.

Protein kinase C phosphorylation site (PS00005 PKC_PHOSPHO_SITE)[8]

[ST]-X-[RK]

Possible protein kinase C phosphorylation sites may be located with the rule shown above. The enzyme exhibits a preference for phosphorylation of serine or threonine residues found in close proximity to C-terminal basic residues. Additional N- or C-terminal basic residues enhance phosphorylation kinetics. As with the glycosylation site, there is no true family per se, and equivalent blocks, profiles, and fingerprints have not been derived.

Protein splicing signature (PS00881 PROTEIN_SPLICING)[8,12,13]

[LIVA]-[LIVMY]-[VAT]-H-N-[STC]

Possible **inteins** may be located with the pattern shown above. Inteins, or protein introns, are parts of protein sequences that are post-translationally excised, their flanking regions (**exteins**) being spliced together to yield an additional protein product. This process is believed to be self-catalysed, apparently initiating at the C-terminal splice junction, where a conserved asparagine residue mediates the nucleophilic attack of the peptide bond between it and its neighbouring residue.

Maximum number of observed repeats: 2. This pattern, which encodes residues close to the asparagine involved in the nucleophilic attack, is a poor discriminator for inteins, finding three times more false positive sequences than true positives. More powerful descriptors are found in the BLOCKS and PRINTS databases, with accession numbers BL00881 and PR00379 respectively.

Domains and modules

Protein domains and modules may be encoded by patterns, blocks, profiles or fingerprints. With the growing numbers of sequences available in databases, deriving effective discriminators for modules has become problematic. Module sequences are often highly divergent and tend not to contain conserved functional residues (module function may vary depending on biological context). Structurally important residues may be hard to detect at the sequence level, and even the number of cysteines, which may stabilize folds by forming disulfide bridges, may vary in a protein family. For this reason, some modules can only be effectively encoded by profiles.

Apple module (PS00495 APPLE)[8,12,13]

C-X(3)-[LIVMFY]-X(5)-[LIVMFY]-X(3)-[DENQ]-[LIVMFY]-X(10)-C-X(3)-C-T-X(4)-C-X-[LIVMFY]-F-X-[FY]-X(13,14)-C-X-[LIVMFY]-[RK]-X-[ST]-X(14,15)-S-G-X-[ST]-[LIVMFY]-X(2)-C

The apple module, shown schematically in Figure 3, is a 90-residue domain stabilized by three disulfide bonds. Multiple tandem repeats of the domain are found in the N termini of the related plasma serine proteases plasma **kallikrein** and coagulation factor XI (*see* **blood coagulation**).

The pattern spans the complete apple module. Maximum number of observed module repeats: 4. Alternative descriptors: BLOCKS accession number BL00495; PRINTS accession number PR00005.

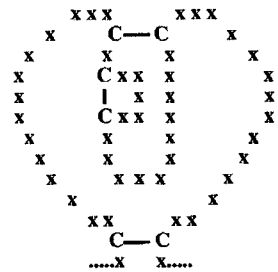

Figure 3. Schematic representation of the apple domain showing the locations of the disulfide linkages. The single-letter amino acid code is used: X denotes any residue.

Cyclic nucleotide-binding domain (PS00888 CNMP_BINDING_1)[8,12,13]

[LIVM]-[VIC]-X(2)-G-[DENQTA]-X-[GA]-X(2)-[LIVMFY](4)-X(2)-G

Proteins that bind cyclic nucleotides (cAMP or cGMP) share a structural domain of around 120 residues. The domain is constructed from three alpha-helices and a distinctive eight-stranded, anti-parallel beta-barrel. Six invariant residues characterize the domain, three of which are glycines thought to be

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essential for maintenance of the structural integrity of the barrel.

This pattern spans beta-strands 2 and 3, and contains the first two conserved glycines. Maximum number of observed domain repeats: 2. Alternative descriptors: BLOCKS accession number BL00888; PRINTS accession number PR00103.

DEAD box (PS00039 DEAD_ATP_HELICASE)[8,13]

[LIVMF](2)-D-E-A-D-[RKEN]-X-[LIVM-FYGSTN]

A number of eukaryotic and prokaryotic proteins involved in ATP-dependent nucleic-acid unwinding have been characterized on the basis of structural similarity. All share a number of conserved motifs, one of which (the so-called 'DEAD box') represents a special version of the B motif of ATP-binding proteins.

This pattern spans the DEAD-box motif. Alternative descriptor: BLOCKS accession number BL00039.

DAG/PE-binding domain (PS00479 DAG_PE_BINDING_DOMAIN)[8,12,13]

H-X-[LIVMFYW]-X(10,11)-C-X(2)-C-X(3)-[LIVMF]-X(2,7)-[SAGC]-[LIVMFYW]-X-C-X(2)-C-X(4)-H-X(2)-C-X(6,7)-C

The N-terminal region of protein kinase C binds phorbol esters (PEs) and diacylglycerol (DAG) in a phospholipid-dependent manner. DAG is an important second messenger; PEs, which are analogues of DAG, are potent tumour promoters that cause several physiological changes when administered to cells and tissues. The DAG/PE-binding domain is characterized by a 50-residue cysteine-rich region, which binds two zinc ions. The metal-ion ligands are thought to be provided by six conserved cysteines and two histidines.

This pattern spans the complete DAG/PE domain. Maximum number of observed domain repeats: 2. Alternative descriptors: BLOCKS accession number BL00479; PRINTS accession number PR00008.

Kringle module (PS00021 KRINGLE)[8,12,13]

[FY]-C-R-N-P-[DNR]

Kringle modules are autonomous structural units found throughout the blood clotting and fibrinolytic proteins. They are believed to play roles in binding mediators (e.g., membranes, other proteins or phospholipids) and in regulating proteolytic activity. Kringles (so-called because cartoon representations of their primary structures resemble Danish pastries of this name) are characterized by a triple loop, three-disulfide-bridge structure, whose conformation is defined by a number of hydrogen bonds and small pieces of antiparallel beta-sheet.

The pattern encodes a well-conserved hexapeptide towards the centre of the kringle domain. Maximum number of observed module repeats: 38. Alternative descriptors: BLOCKS accession number BL00021; PRINTS accession number PR00018.

P-type 'trefoil' module (PS00025 P_TREFOIL)[8,13]

R-X(2)-C-X-[FYPST]-X(3,4)-[ST]-X(3)-C-X(4)-C-C-[FYWH]

Figure 4. Schematic representation of disulfide linkages that form the P-domain. The single-letter amino acid code is used: x denotes any residue; Φ indicates the presence of large hydrophobic residues; @ marks the location of the pattern.

The P-type 'trefoil' module (or P-domain) is a 45-residue cysteine-rich region, the six cysteines of which form disulfide bridges in the order 1–5, 2–4, 3–6, as illustrated schematically in Figure 4. The domain has been found in a variety of extracellular eukaryotic proteins.

The pattern encodes the central four cysteine residues. Maximum number of observed module repeats: 6. Alternative descriptor: BLOCKS accession number BL00025.

WW module (PS01159 WW_DOMAIN_1)[8,12,13]

W-X(9,11)-[VFY]-[FYW]-X(6,7)-[GSTNE]-[GSTQCR]-[FYW]-X(2)-P

WW modules are conserved 35–40 residue regions found in a number of disparate proteins. The domain is characterized by two conserved tryptophan residues and a conserved proline (hence its alternative name, WWP). Among the proteins known to contain WW domains is **dystrophin**, the product encoded by the gene responsible for Duchenne muscular dystrophy. The domain appears to bind proteins that contain characteristic proline motifs ([AP]-P-P-[AP]-Y), and, to an extent, resembles SH3 domains. It is often associated with other domains that typify proteins involved in signal transduction.

This pattern spans the full WW domain. Maximum number of observed module repeats: 4. Alternative descriptors: BLOCKS accession number BL01159; PRINTS accession number PR00403; PROSITE profile accession number PS50020.

Zinc finger (C_2H_2 type) domain (PS00028 ZINC_FINGER_C2H2)[8,12,13]

C-X(2,4)-C-X(3)-[LIVMFYWC]-X(8)-H-X(3,5)-H

Zinc fingers are small, self-folding units in which zinc is a crucial structural component. The finger contains a repeated 28-residue sequence, including two conserved cysteine and two conserved histidine residues in a C-X(2)-C-X(12)-H-X(3)-H type motif. The 12 residues separating the second cysteine and the first histidine are largely polar and basic, implicating this

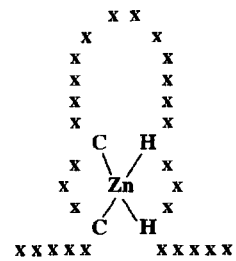

Figure 5. Schematic representation of zinc coordination by the C_2H_2-type zinc finger. The single-letter amino acid code is used: x denotes any residue.

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region in particular in nucleic-acid binding. A single atom of zinc is bound in a tetrahedral array to yield a finger-like projection (shown schematically in Figure 5), which interacts with nucleotides in the major groove of the nucleic acid – the zinc binds to the conserved cysteine and histidine residues. Fingers have been found to bind to about five base pairs of nucleic acid containing short runs of guanine residues. They are found in all transcription factors, and also in proteins such as RNA and DNA polymerases. The ability to bind to both RNA and DNA suggests versatility not demonstrated by the helix-turn-helix motif: the zinc finger may thus represent the original nucleic-acid binding protein.

The pattern encodes the cysteine and histidine ligands. Maximum number of observed finger repeats: 37. Alternative descriptors: BLOCKS accession number BL00028; PRINTS accession number PR00048.

Protein families

Protein families may be effectively encoded by patterns, blocks, profiles, or fingerprints. Some typical examples are given below.

Short-chain alcohol dehydrogenases (PS00061 ADH_SHORT)[8,12,13]

[LIVSPADK]-X(12)-Y-[PSTAGNCV]-[STAGNQCIVM]-[STAGC]-K-{PC}-[SAGFR]-[LIVMTAGD]-X(2)-[LIVMFYW]-X(3)-[LIVMFWGAPTH]-[GSACQRHM]

Primary sequence comparisons indicate an evolutionary relationship between many dehydrogenases. Most dehydrogenases possess at least two domains, the first binding the coenzyme (often NAD), and the second binding the substrate. This latter domain determines the substrate specificity and contains amino acids involved in catalysis. Little sequence similarity has been found in the coenzyme-binding domain, although there is a large degree of structural similarity. It is thus postulated that the dehydrogenase structure has arisen through gene fusion of a common ancestral coenzyme nucleotide sequence with various substrate-specific domains. A number of short conserved regions characterize the alcohol dehydrogenases, one of which includes two perfectly conserved residues: a tyrosine and a lysine. In glucose dehydrogenase, the tyrosine has been shown to be important for catalytic activity and/or for subunit binding.

The pattern encodes the functionally important tyrosine and lysine residues. Maximum number of observed repeats: 2. Alternative descriptors: BLOCKS accession number BL00061; PRINTS accession number PR00080.

Lipocalin signature (PS00213 LIPOCALIN)[8,12,13]

[DENG]-X-[DENQGSTARK]-X(0,2)-[DENQARK]-[LIVFY]-{CP}-G-{C}-W-[FYWLRH]-X-[LIVMTA]

The lipocalins are primarily a family of extracellular ligand-binding proteins that display high specificity for small hydrophobic molecules. Their functions include transport of nutrients, control of cell regulation, pheromone transport, cryptic coloration, and the enzymatic synthesis of prostaglandins. The structure shows a novel, eight-stranded, antiparallel beta-barrel fold. Sequence similarity is low, and appears to be restricted to conserved disulfides and three motifs, which form a juxtaposed cluster that may act as a common cell-surface receptor site. The antiparallel beta-barrel fold is similarly exploited by the fatty-acid-binding proteins, which also bind small hydrophobic molecules. Similarity at the sequence level is less obvious, being confined to a single short N-terminal motif.

This pattern encodes the N-terminal motif that characterizes both the lipocalins and fatty-acid-binding proteins. More powerful descriptors: BLOCKS accession number BL00213; PRINTS accession number PR00179.

G-protein-coupled receptors (PS00237 G_PROTEIN_RECEPTOR)[8,12,13]

[GSTALIVMFYWC]-[GSTANCPDE]-{EDPKRH}-X(2)-[LIVMNQGA]-X(2)-[LIVMFT]-[GSTANC]-[LIVMFYWSTAC]-[DENH]-R-[FYWCSH]-X(2)-[LIVM]

G-protein-coupled receptors (GPCRs) constitute a vast protein family encompassing a wide range of functions (including various autocrine, paracrine, and endocrine processes). They show considerable diversity at the sequence level, on the basis of which they can be separated into distinct families. These families belong to a clan, within which there are indications of an evolutionary relationship, but between members of which there is no statistically significant similarity in sequence. The currently known clan members include the rhodopsin-like GPCRs, the secretin-like GPCRs, the cAMP receptors, the fungal pheromone mating factor receptors, and the metabotropic glutamate receptor family.

The rhodopsin-like GPCRs themselves represent a widespread protein family that includes hormone, neurotransmitter, and light receptors, all of which transduce extracellular signals through interaction with guanine nucleotide-binding (G) proteins. Although their activating ligands vary widely in structure and character, the amino-acid sequences of the receptors are very similar and are believed to adopt a common structural framework comprising seven transmembrane helices.

This pattern encodes part of the third transmembrane domain, which contains a completely conserved arginine residue that is implicated in binding the G-protein. More powerful descriptors: BLOCKS accession number BL00237; PRINTS accession number PR00237.

Primary databases

Nucleic acid and protein sequences are stored in primary databases. The principal primary resources are (for proteins) PIR, SWISS-PROT, mips, PSD-KYOTO, PRF, and NRL-3D and (for nucleic acids) EMBL, GenBank, and DDBJ. There are, of course, many others.

The proliferation of primary databases causes problems: do they all have the same format? Which is the most accurate? Which is the most up-to-date? Which is the most comprehensive? Which should we use?

SWISS-PROT is often regarded as the 'best', at least in terms of the quality of its annotations. But its sequence data are taken from PIR, compared with which it is neither as comprehensive, nor as up-to-date. NRL-3D is derived from the Brookhaven protein structure databank, so contains only se-

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quences for which three-dimensional coordinates have been made available – it is therefore only small, and highly redundant, yet in view of the link it provides to structure, it is nevertheless a valuable resource. In the past, choosing which database to use was largely a matter of which was available locally. Nowadays, the problem is more likely to be a question of finding the right WWW page to allow you to perform the relevant search. In practice, to ensure the most comprehensive search, it is best to search several sources.

Cooperative projects

Maintaining databases is a laborious, time-consuming process. To relieve some of the inherent burdens, a number of groups have cooperated to share data: for protein sequences, PIR, mips, and PSD-KYOTO join forces as PIR-International; for nucleic-acid sequences, EMBL, GenBank, and DDBJ pool their resources.

Composite databases

Cooperative projects help with data distribution, but do not address the problem of multiple database formats. One approach to tackling proliferating primary databases is to compile a composite resource. Here, data from a variety of different sources are merged, rendering searches extremely efficient, the more so if redundancies between contributing sources are eliminated. But the situation is complicated by the fact that there are now several composites available (see Table 1), each of which uses different data sources, has a different format, and uses different redundancy criteria.

Table 1. Examples of composite protein sequence databases

Database	Data sources
nrdb	PDB, PIR, SWISS-PROT, GenPept, GenPept updates
Entrez	PDB, PIR, SWISS-PROT, PRF
mipsX	PIR, mips, patchX, PSD-KYTO
OWL	SWISS-PROT, PIR, GenBank, NRL-3D

Of the available composite databases, the nrdb, Entrez, and mipsX resources are in fact non-identical. Only OWL is truly non-redundant, in the sense that strict redundancy criteria are applied to the amalgamation of the primary sources (i.e., both identical and trivially different sequences are eliminated). OWL is therefore relatively small and hence efficient in database searching. But it is not as up-to-date as, for example, nrdb. So again, the user is faced with the choice of which is best to use. In practice, the ease of use of the Web makes it possible to search them all.

Secondary databases

Secondary databases contain information derived from the primary sources. There are numerous secondary, or 'value-added', databases available, all of which have different formats, use different analysis methods, and house different types of information, and most of which use different data sources (although SWISS-PROT is emerging as something like a standard) – see Table 2.

As with the primary sources, the proliferation of secondary databases causes problems: Which is the most accurate? Which is the most up-to-date? Which is the most comprehensive? Which should we use?

PROSITE is the most widely used resource. It houses a comprehensive array of patterns, rules and profiles, encoding a variety of functional sites, domains and families. In most cases, it provides good annotations and links to other biological databases, yet diagnostically it is probably the least reliable. The profile library is still small, but profiles provide much better discrimination than can patterns. Similarly, the BLOCKS database is a more powerful resource than PROSITE, but it provides no additional annotation, and, because it is derived from families identified in PROSITE, it offers no further family coverage. The PRINTS fingerprint database does provide family signatures not seen in PROSITE and offers more powerful discrimination, yet it is not as comprehensive. The situation is similar for its BLOCKS-format counterpart (strictly a tertiary database, as it is derived from secondary data), which provides even more potent discriminators.

Table 2. Examples of secondary databases

Database	Data source	Information stored
PROSITE	SWISS-PROT	patterns, rules, profiles
Profiles	SWISS-PROT	weight matrices
BLOCKS	SWISS-PROT, PROSITE	clustered, weighted motifs
PRINTS	OWL	unweighted motifs
BLOCKS-format-PRINTS	PRINTS	clustered, weighted motifs
ProDom	SWISS-PROT	domain alignments
SBASE	SWISS-PROT	annotated domain sequences
Pfam*	SWISS-PROT	annotated alignments
PIMA	Entrez	marked-up alignments

*Pfam is bases on probabilistic Hidden Markov Model.

The ProDom, SBASE, Pfam, and PIMA databases effectively contain marked-up domain sequences and alignments, derived from largely automated processes, rather than the descriptors housed in these other resources. They provide no supporting documentation and, diagnostically, are often unreliable. Nevertheless, in a comprehensive search protocol, it is wise to include as many secondary databases as possible, as no single resource can yet guarantee a diagnosis.

Information networks

Progress in bioinformatics would not have been possible without the international computer network, the Internet. The 'universe of network-accessible information' has been dubbed the World Wide Web, an 'embodiment of human knowledge'! Participating groups make information available on servers, all of which have unique addresses, referred to as Uniform Resource Locators, or URLs. Armed with a URL and a suitable WWW browser (e.g., Netscape, Mosaic, or Lynx), users may visit any site in the world and use the tools and data made available by those institutions or organizations. The URLs of some of the resources discussed above are given in Table 3.

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Table 3. World Wide Web addresses of various bioinformatics resources

Database/resource	Reference	URL
SWISS-PROT	1	http://expasy.hcuge.ch/sprot/sprot-top.html
PIR	2	http://www.gdb.org/Dan/proteins/pir.html
mips	2	http://www.mips.biochem.mpg.de/
PRF		http://www.genome.ad.jp/htbin/bfind_prf
NRL-3D	3	http://www.gdb.org/Dan/proteins/nrl3d.html
GenBank	4	http://www.ncbi.nlm.nih.gov/
EMBL	5	http://www.ebi.ac.uk/ebi_docs/embl_db/ebi/topembl.html
OWL	6	http://www.biochem.ucl.ac.uk/bsm/dbbrowser/OWL/OWL.html
nrdb	4	http://www.ncbi.nlm.nih.gov/BLAST/blast_databases.html
Entrez	7	http://www3.ncbi.nlm.nih.gov/Entrez/
PROSITE	8	http://expasy.hcuge.ch/sprot/prosite.html
Profiles	9	http://ulrec3.unil.ch/profile/profile.html
ProDom	10	http://www.sanger.ac.uk/~esr/prodom.html
SBASE	11	http://base.icgeb.trieste.it/sbase/
PRINTS	12	http://www.biochem.ucl.ac.uk/bsm/dbbrowser/PRINTS/PRINTS.html
BLOCKS	13	http://www.blocks.fhcrc.org/
PIMA	14	http://dot.imgen.bcm.tmc.edu:9331/seq-search/Help/beauty.html
Pfam		http://www.sanger.ac.uk/Pfam/
PDB	15	http://www.genome.ad.jp/htbin/bfind_pdb
SCOP	16	http://scop.mrc-lmb.cam.ac.uk/scop/
CATH	17	http://www.biochem.ucl.ac.uk/bsm/cath/
PROSITE.lis		http://expasy.hcuge.ch/cgi-bin/prosite-list.pl
PRINTS.lis		http://www.biochem.ucl.ac.uk/bsm/dbbrowser/PRINTS/printscontents.html
PROFILES.lis		http://ulrec3.unil.ch/cgi-bin/PFSCAN_form_parser2
Protfam		http://www.mips.biochem.mpg.de/public/protfam/fbrowser.html
Pfam		http://www.sanger.ac.uk/Pfam/browse_curr.html
Modules		http://swan.embl-heidelberg.de:8080/Modules/

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Appendix F

Restriction enzymes and methylases

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The restriction enzyme database, REBASE, is a collection of information about restriction enzymes and methylases (1). Recently, homing endonucleases (2) have also been included in REBASE. Among the 2825 restriction enzymes now known, there are 18 fully characterized Type I specificities, 210 different Type II specificities and 4 different Type III specificities. Tables 1–3 contain a listing of all prototype restriction enzymes (Types I, II, and III), together with their commercially available isoschizomers and neoschizomers. Table 4 contains a listing of the 23 homing endonucleases for which recognition sequences are available. REBASE currently stores 3959 published references, which include abstracts, and 464 unpublished observations.

REBASE is updated daily. Each month, a set of REBASE data files are released publicly and distributed to the scientific community, at no charge, via e-mail. They can also be retrieved by anonymous ftp (`www.neb.com, in pub/rebase`), WAIS (`www.neb.com, port 210`) or through the World Wide Web (`http://www.neb.com/rebase`). These data files are ASCII text files, many of which are designed specifically for use with a variety of software packages such as GCG, IGSuite, GENEPRO, Staden, DNA Strider, Pro-Cite, PC/Gene, SEQAIDII, GENETYX, DNASIS, CAD Gene, and Reference Manager. Other data files include a complete set of references, including abstracts, to papers on restriction enzymes and methylases; a list of all commercial suppliers of restriction enzymes and methylases, complete with contact information and a listing of enzymes they currently sell. New data files are constantly being added and each release of REBASE includes a monthly newsletter indicating that the files at the WWW and ftp sites have been updated, and listing new enzymes, newly available formats, enzyme name changes, etc. To join the mailing list or for more information, contact either author (e-mail: `macelis@neb.com` or `roberts@neb.com`; telephone (508) 927-3382; fax (508) 921-1527).

In forming Tables 1–3, all endonucleases cleaving DNA at a specific sequence have been considered to be restriction enzymes, although in most cases there is no direct genetic evidence for the presence of a restriction-modification system. The endonucleases are named in accordance with the proposal of Smith and Nathans (3).

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Appendix F

Table 1. Type II enzymes

Prototype	Isoschizomers	Recognition sequence[1]	Me site[2]	Commercial source[3]
*Aat*II		GACGT↑C		ADEFKLMNOPRS
*Acc*I		GT↑MKAC	5(6)	ABDEGJKLMNOPQRS
*Ace*III		CAGCTC(7/11)		
*Aci*I		CCGC(–3/–1)		N
*Acl*I		AA↑CGTT		I
	*Psp*1406I	AA↑CGTT		DFMN
*Acy*I		GR↑CGYC		JM
	*Bbi*II	GR↑CGYC		K
	*Bst*ACI	GR↑CGYC		I
	*Bsa*HI	GR↑CGYC		NS
	*Hin*1I	GR↑CGYC		EFO
	*Hsp*92I	GR↑CGYC		R
	*Msp*17I	GR↑CGYC		D
*Afl*II		C↑TTAAG		ABJKNOS
	*Bfr*I	C↑TTAAG		MO
	*Bsp*TI	C↑TTAAG		DF
	*Bst*98I	C↑TTAAG		R
	*Msp*CI	C↑TTAAG		C
	*Vha*464I	C↑TTAAG		I
*Afl*III		A↑CRYGT		ABMN
*Age*I		A↑CCGGT	?(5)	JNR
	*Asi*AI	A↑CCGGT		I
	*Pin*AI	A↑CCGGT		BM
*Aha*III		TTT↑AAA		
	*Dra*I	TTT↑AAA		ABDEFGIJKLMNOPQRS
*Alu*I		AG↑CT	3(5)	ABCDEFGHIJKLMNOPQRST
*Alw*NI		CAGNNN↑CTG		ABNS
*Apa*I		GGGCC↑C	4(5)	ABEGIJKLMNOPQRS
	*Bsp*120I	G↑GGCCC		DFN
	*Psp*OMI	G↑GGCCC		I
*Apa*BI		GCANNNNN↑TGC		
*Apa*LI		G↑TGCAC	?(5)	ADEKNS
	*Alw*44I	G↑TGCAC		FJMOR
	*Vne*I	G↑TGCAC		I
*Apo*I		R↑AATTY	?(6)	N
	*Acs*I	R↑AATTY		DIM
*Asc*I		GG↑CGCGCC	?(5)	N
*Asu*I		G↑GNCC		
	*Asp*S9I	G↑GNCC		I
	*Bsi*ZI	G↑GNCC		T
	*Cfr*13I	G↑GNCC	4(5)	DFKO
	*Fmu*I	GGNC↑C		
	*Sau*96I	G↑GNCC	4(5)	AJLMNORS
*Asu*II		TT↑CGAA		
	*Bpu*14I	TT↑CGAA		I
	*Bsi*CI	TT↑CGAA		T
	*Bsp*119I	TT↑CGAA		DF
	*Bst*BI	TT↑CGAA		NS
	*Cbi*I	TT↑CGAA		J

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Table 1 cont.

Prototype	Isoschizomers	Recognition sequence[1]	Me site[2]	Commercial source[3]
	*Csp*45I	TT↑CGAA		OR
	*Lsp*I	TT↑CGAA		L
	*Nsp*V	TT↑CGAA		ABJKO
	*Sfu*I	TT↑CGAA		M
*Ava*I		C↑YCGRG	?(4)	ABEGJKLMNOPQRS
	*Ama*87I	C↑YCGRG		DI
	*Bco*I	C↑YCGRG		AT
	*Bso*BI	C↑YCGRG	?(4)	N
	*Eco*88I	C↑YCGRG		F
	*Nli*387/7I	CYCGR↑G		
*Ava*II		G↑GWCC	?(5)	ABEGJKMNPQRS
	*Bme*18I	G↑GWCC		I
	*Eco*47I	G↑GWCC		FO
	*Hgi*EI	G↑GWCC	?(5)	D
	*Sin*I	G↑GWCC	4(5)	LR
	*Vpa*K11AI	↑GGWCC		
*Ava*III		ATGCAT		
	*Bfr*BI	ATG↑CAT		
	*Eco*T22I	ATGCA↑T		AKO
	*Mph*1103I	ATGCA↑T		F
	*Nsi*I	ATGCA↑T		BDEHJLMNRS
	*Ppu*10I	A↑TGCAT		DFN
	*Zsp*2I	ATGCA↑T		I
*Avr*II		C↑CTAGG		N
	*Bln*I	C↑CTAGG		AKM
	*Bsp*A2I	C↑CTAGG		I
*Bae*I[4]		(10/15)ACNNNNGTAYC(12/7)	1(6),–4(6)	
*Bal*I		TGG↑CCA	4(4)	AJKR
	*Mlu*NI	TGG↑CCA		M
	*Msc*I	TGG↑CCA		BDNOS
*Bam*HI		G↑GATCC	5(4)	ABCDEFGHIJKLMNOPQRST
*Bbv*I		GCAGC(8/12)	2(5),–2(5)	N
	*Bst*71I	GCAGC(8/12)		R
*Bbv*II		GAAGAC(2/6)		
	*Bbs*I	GAAGAC(2/6)		N
	*Bpi*I	GAAGAC(2/6)		DF
	*Bpu*AI	GAAGAC(2/6)		M
*Bcc*I		CCATC		
*Bce*83I		CTTGAG(16/14)		
*Bce*fI		ACGGC(12/13)		
*Bcg*I5		(10/12)CGANNNNNNTGC(12/10)	3(6),–3(6)	N
*Bci*VI		GGATAC (6/5)		N
*Bcl*I		T↑GATCA		BCDEFGJLMNOPRS
	*Bsi*QI	T↑GATCA		T
	*Fba*I	T↑GATCA		AK
	*Ksp*22I	T↑GATCA		I
*Bet*I		W↑CCGGW		
	*Bsa*WI	W↑CCGGW		N
*Bfi*I		ACTGGG(4/5)		F
*Bgl*I		GCCNNNN↑NGGC	?(4)	ABCDEFGHIJKLMNOPQRST

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Appendix F

Table 1 cont.

Prototype	Isoschizomers	Recognition sequence[1]	Me site[2]	Commercial source[3]
*Bgl*II		A↑GATCT	5(4)	ABCDEFGHIJKLMNOPQRST
*Bin*I		GGATC(4/5)		
	*Acl*WI	GGATC(4/5)		I
	*Alw*I	GGATC(4/5)		NS
*Bmg*I		GKGCCC		
*Bpl*I		GAGNNNNNCTC		
*Bpu*10I		CCTNAGC(–5/–2)		
*Bsa*AI		YAC↑GTR		N
	*Bs+t*BAI	YAC↑GTR		I
*Bsa*BI		GATNN↑NNATC		N
	*Bse*8I	GATNN↑NNATC		I
	*Bsh*1365I	GATNN↑NNATC		DF
	*Bsi*BI	GATNN↑NNATC		T
	*Bsr*BRI	GATNN↑NNATC		R
	*Mam*I	GATNN↑NNATC	?(6)	M
*Bsa*XI		ACNNNNNCTCC		
*Bsb*I		CAACAC		
*Bsc*GI		CCCGT		
*Bse*PI		G↑CGCGC		I
	*Bss*HII	G↑CGCGC	?(5)	ABDEJKLMNOPQR
	*Pau*I	G↑CGCGC		F
*Bse*RI		GAGGAG(10/8)		N
*Bsg*I		GTGCAG(16/14)		N
*Bsi*I		CACGAG(–5/–1)		
	*Bss*SI	CACGAG(–5/–1)		N
	*Bst*2BI	CACGAG(–5/–1)		DI
*Bsi*YI		CCNNNNN↑NNGG		MT
	*Bsc*4I	CCNNNNN↑NNGG		I
	*Bsl*I	CCNNNNN↑NNGG		N
*Bsm*I		GAATGC(1/–1)		ABDEJLMNOS
	*Bsa*MI	GAATGC(1/–1)		R
	*Bsc*CI	GAATGC(1/–1)		T
	*Mva*1269I	GAATGC(1/–1)		F
*Bsm*AI		GTCTC(1/5)		N
	*Alw*26I	GTCTC(1/5)	3(5),–4(6)	DFNR
*Bsp*24I5		(8/13)GACNNNNNNTGG(12/7)		
*Bsp*1407I		T↑GTACA		DF
	*Bsr*GI	T↑GTACA		N
	*Ssp*BI	T↑GTACA		M
*Bsp*GI		CTGGAC		
*Bsp*HI		T↑CATGA		AN
	*Rca*I	T↑CATGA		BM
*Bsp*LU11I		A↑CATGT		M
*Bsp*MI		ACCTGC(4/8)		N
*Bsp*MII		T↑CCGGA		
	*Acc*III	T↑CCGGA		EJKQR
	*Bse*AI	T↑CCGGA		CM
	*Bsi*MI	T↑CCGGA		AT
	*Bsp*13I	T↑CCGGA		I
	*Bsp*EI	T↑CCGGA		N

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Table 1 cont.

Prototype	Isoschizomers	Recognition sequence[1]	Me site[2]	Commercial source[3]
	*Kpn*2I	T↑CCGGA		BDF
	*Mro*I	T↑CCGGA		MO
*Bsr*I		ACTGG(1/–1)		N
	*Bse*1I	ACTGG(1/–1)		I
	*Bse*NI	ACTGG(1/–1)		DF
	*Bsr*SI	ACTGG(1/–1)		R
*Bsr*BI		CCGCTC(–3/–3)		N
	*Acc*BSI	CCGCTC(–3/–3)		DI
*Bsr*DI		GCAATG(2/0)		N
	*Bse*3DI	GCAATG(2/0)		I
*Bst*EII		G↑GTNACC		BDGHJLMNORS
	*Bst*PI	G↑GTNACC		K
	*Eco*91I	G↑GTNACC		F
	*Eco*O65I	G↑GTNACC		AK
	*Psp*EI	G↑GTNACC		I
*Bst*XI		CCANNNNNN↑NTGG		ABDEFGHJKLMNOQRS
*Cac*8I		GCN↑NGC		N
*Cau*II		CC↑SGG		
	*Asu*C2I	CC↑SGG		I
	*Bcn*I	CC↑SGG	2(4)	ADFK
	*Eco*HI	↑CCSGG		
	*Nci*I	CC↑SGG		BEJLMNORST
*Cfr*I		Y↑GGCCR	4(5)	F
	*Eae*I	Y↑GGCCR	4(5)	ADKLMNS
*Cfr*10I		R↑CCGGY	2(5)	ADFKMO
	*Bse*118I	R↑CCGGY		I
	*Bsr*FI	R↑CCGGY		N
	*Bss*AI	R↑CCGGY		C
*Cje*I[4]		(8/14)CCANNNNNNGT(15/9)		
*Cje*PI[4]		(7/13)CCANNNNNNNTC(14/8)		
*Cla*I		AT↑CGAT	5(6)	ABKMNPRST
	*Ban*III	AT↑CGAT		O
	*Bsa*29I	AT↑CGAT		I
	*Bsc*I	AT↑CGAT		L
	*Bse*CI	AT↑CGAT	5(6)	C
	*Bsi*XI	AT↑CGAT		T
	*Bsp*106I	AT↑CGAT	5(6)	E
	*Bsp*DI	AT↑CGAT		N
	*Bsp*XI	AT↑CGAT		G
	*Bsu*15I	AT↑CGAT	5(6)	DF
*Cvi*JI		RG↑CY	3(5)	Q
*Cvi*RI		TG↑CA	4(6)	
*Dde*I		C↑TNAG	1(5)	ABEGLMNOR
	*Bst*DEI	C↑TNAG		DI
*Dpn*I[5]		GmA↑TC		ABLMNRS
*Dra*II		RG↑GNCCY		AGMS
	*Eco*O109I	RG↑GNCCY		ABDEFJKLN
	*Pss*I	RGGNC↑CY		
*Dra*III		CACNNN↑GTG		AEGMNS
*Drd*I		GACNNNNN↑NNGTC		N

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Appendix F

Table 1 cont.

Prototype	Isoschizomers	Recognition sequence[1]	Me site[2]	Commercial source[3]
	*Dse*DI	GACNNNN↑NNGTC		I
*Drd*II		GAACCA		
*Dsa*I		C↑CRYGG		M
	*Bst*DSI	C↑CRYGG		DI
*Eam*1105I		GACNNN↑NNGTC		DFK
	*Ahd*I	GACNNN↑NNGTC		N
	*Asp*EI	GACNNN↑NNGTC		M
	*Ecl*HKI	GACNNN↑NNGTC		R
	*Nru*GI	GACNNN↑NNGTC		I
*Eci*I		TCCGCC		
*Eco*31I		GGTCTC(1/5)	4(5),–4(6)	DF
	*Bsa*I	GGTCTC(1/5)		N
*Eco*47III		AGC↑GCT		BDEFLMNOR
	*Afe*I	AGC↑GCT		I
	*Aor*51HI	AGC↑GCT		AK
*Eco*57I		CTGAAG(16/14)	5(6),–5(6)	DFNS
*Eco*NI		CCTNN↑NNNAGG		ANS
*Eco*RI		G↑AATTC	3(6)	ABCDEFGHIJKLMNOPQRST
*Eco*RII[6]		↑CCWGG	2(5)	BEJMOS
+	*Bsi*LI	CC↑WGG		T
+	*Bst*NI	CC↑WGG	2(4)	CENS
+	*Bst*OI	CC↑WGG		R
+	*Bst*2UI	CC↑WGG		I
+	*Mva*I	CC↑WGG	2(4)	ADFKMO
*Eco*RV		GAT↑ATC	2(6)	ABCDEGHIJKLMNOPQRST
	*Eco*32I	GAT↑ATC		F
*Esp*I		GC↑TNAGC		
	*Blp*I	GC↑TNAGC		N
	*Bpu*1102I	GC↑TNAGC		BDEFK
	*Bsp*1720I	GC↑TNAGC		I
	*Cel*II	GC↑TNAGC		ALM
*Esp*3I		CGTCTC(1/5)	4(5),–4(6)	DF
	*Bsm*BI	CGTCTC(1/5)		N
*Fau*I		CCCGC(4/6)		I
*Fin*I		GGGAC		
	*Bsm*FI	GGGAC(10/14)		N
*Fnu*DII		CG↑CG		
	*Acc*II	CG↑CG		AJKQ
	*Bsh*1236I	CG↑CG		DEF
	*Bst*UI	CG↑CG		NS
	*Mvn*I	CG↑CG		M
	*Sel*I	↑CGCG		
	*Tha*I	CG↑CG		B
*Fnu*4HI		GC↑NGC		N
	*Bso*FI	GC↑NGC		N
	*Fsp*4HI	GC↑NGC		I
	*Ita*I	GC↑NGC		M
*Fok*I		GGATG(9/13)	3(6),–2(6)	ADGIJKLMNRS
	*Bst*F5I	GGATG(2/0)		I
	*Sts*I	GGATG(10/14)	3(6),–2(6)	

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Table 1 cont.

Prototype	Isoschizomers	Recognition sequence[1]	Me site[2]	Commercial source[3]
*Fse*I		GGCCGG↑CC	?(5)	AKN
*Gdi*II		CGGCCR(–5/–1)		
*Gsu*I		CTGGAG(16/14)		DFS
	*Bpm*I	CTGGAG(16/14)		N
*Hae*I		WGG↑CCW		
*Hae*II		RGCGC↑Y		ABDEGJKLMNORS
	*Bsp*143II	RGCGC↑Y		F
	*Bst*H2I	RGCGC↑Y		I
	*Lpn*I	RGC↑GCY		
*Hae*III		GG↑CC	3(5)	ABCDGHIJKLMNOPQRST
	*Bsh*I	GG↑CC		T
	*Bsu*RI	GG↑CC	3(5)	FI
	*Pal*I	GG↑CC		E
*Hga*I		GACGC(5/10)	3(5),–2(5)	AN
*Hgi*AI		GWGCW↑C		
	*Alw*21I	GWGCW↑C		DF
	*Asp*HI	GWGCW↑C		M
	*Bbv*12I	GWGCW↑C		I
	*Bsi*HKAI	GWGCW↑C		N
*Hgi*CI		G↑GYRCC	5(5)	
	*Acc*B1I	G↑GYRCC		I
	*Ban*I	G↑GYRCC	?(5)	AEMNORS
	*Bsh*NI	G↑GYRCC		F
	*Eco*64I	G↑GYRCC		DF
*Hgi*EII		ACCNNNNNNGGT		
*Hgi*JII		GRGCY↑C		
	*Ban*II	GRGCY↑C	4(5)	ABKLMNOQRS
	*Eco*24I	GRGCY↑C		DF
	*Eco*T38I	GRGCY↑C		J
	*Fri*OI	GRGCY↑C		I
*Hha*I		GCG↑C	2(5)	ABGJKNOPRS
	*Asp*LEI	GCG↑C		I
	*Cfo*I	GCG↑C		BLMRS
	*Hin*6I	G↑CGC		DF
	*Hin*P1I	G↑CGC		N
	*Hsp*AI	G↑CGC		I
*Hin*4I		GABNNNNNVTC		
*Hin*dII		GTY↑RAC	5(6)	EM
	*Hin*cII	GTY↑RAC	5(6)	ABCDEFGHJKLNOPQRS
*Hin*dIII		A↑AGCTT	1(6)	ABCDEFGHIJKLMNOPQRST
*Hin*fI		G↑ANTC		ABDEFGHIJKLMNOPQRST
*Hpa*I		GTT↑AAC	5(6)	ABDEFGJKLMNOPQRST
	*Bst*HPI	GTT↑AAC		I
*Hpa*II		C↑CGG	2(5)	BDEFGILMNOPQRS
	*Bsi*SI	C↑CGG		C
	*Hap*II	C↑CGG	2(5)	AK
	*Hin*2I	C↑CGG		F
	*Msp*I	C↑CGG	1(5)	ABDEFGHIJKLMNOPQRS
*Hph*I		GGTGA(8/7)	5(6),–2(5)	AFNS
	*Asu*HPI	GGTGA(8/7)		I

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Table 1 cont.

Prototype	Isoschizomers	Recognition sequence[1]	Me site[2]	Commercial source[3]
*Kpn*I		GGTAC↑C	4(6)	ABCDEFGHIJKLMNOPQRST
	*Acc*65I	G↑GTACC		DFINR
	*Asp*718I	G↑GTACC		M
*Ksp*632I		CTCTTC(1/4)		M
	*Bsu*6I	CTCTTC(1/4)		I
	*Eam*1104I	CTCTTC(1/4)		DEF
	*Ear*I	CTCTTC(1/4)		N
*Mae*I		C↑TAG		M
	*Bfa*I	C↑TAG		N
*Mae*II		A↑CGT		M
	*Tai*I	ACGT↑		FN
	*Tsc*I	ACGT↑		L
*Mae*III		↑GTNAC		MP
*Mbo*I[7]		↑GATC	2(6)	ABCEFGKLNQRST
	*Bsc*FI	GATC		T
+	*Bsp*143I	↑GATC		DF
+	*Bsp*KT6I	GAT↑C	2(6)	
	*Cha*I	GATC↑		
	*Dpn*II	↑GATC	2(6)	N
	*Kzo*9I	↑GATC		I
	*Nde*II	↑GATC		BDGJM
+	*Sau*3AI	↑GATC	4(5)	ABEGHJKLMNOPQRS
*Mbo*II		GAAGA(8/7)	5(6)	ABDFGJKNOQRS
*Mcr*I		CGRY↑CG		
	*Bsa*OI	CGRY↑CG		R
	*Bsh*1285I	CGRY↑CG		DF
	*Bsi*EI	CGRY↑CG		N
	*Bst*MCI	CGRY↑CG		I
*Mfe*I		C↑AATTG		N
	*Mun*I	C↑AATTG	3(6)	BDEFKM
*Mlu*I		A↑CGCGT		ABDEFGIJKLMNOPQRS
*Mme*I		TCCRAC(20/18)		
*Mnl*I		CCTC(7/6)		AEFNQ
*Mse*I		T↑TAA		BN
	*Tru*1I	T↑TAA		F
	*Tru*9I	T↑TAA		DILMRS
*Msl*I		CAYNN↑NNRTG		N
*Mst*I		TGC↑GCA		
	*Acc*16I	TGC↑GCA		DI
	*Avi*II	TGC↑GCA		M
	*Fsp*I	TGC↑GCA		ABJKNOS
*Mwo*I		GCNNNNN↑NNGC	?(5)	N
*Nae*I		GCC↑GGC		ADEKLMNOR
	*Mro*NI	G↑CCGGC		I
	*Ngo*AIV	G↑CCGGC		B
	*Ngo*MI	G↑CCGGC	2(5)	NR
*Nar*I		GG↑CGCC		BEJMNOPRS
	*Bbe*I	GGCGC↑C		AK
	*Ege*I	GGC↑GCC		I
	*Ehe*I	GGC↑GCC		ADFNO

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Table 1 cont.

Prototype	Isoschizomers	Recognition sequence[1]	Me site[2]	Commercial source[3]
	*Kas*I	G↑GCGCC		N
	*Mly*113I	GG↑CGCC		I
*Nco*I		C↑CATGG	?(4)	ABCDEFGHJKLMNOPQRST
	*Bsp*19I	C↑CATGG		I
*Nde*I		CA↑TATG		ABDEFGJKLMNPRS
	*Fau*NDI	CA↑TATG		DI
*Nhe*I		G↑CTAGC		ABDEFGJKLMNOPRS
	*Ace*II	GCTAG↑C		
	*Asu*NHI	G↑CTAGC		I
*Nla*III		CATG↑	2(6)	ANOS
	*Cvi*AII	C↑ATG	2(6)	
	*Hsp*92II	CATG↑		R
*Nla*IV		GGN↑NCC		NS
	*Bsc*BI	GGN↑NCC		T
	*Bsp*LI	GGN↑NCC		F
	*Psp*N4I	GGN↑NCC		I
*Not*I		GC↑GGCCGC	?(4)	ABCDEFGJKLMNOPQRST
	*Cci*NI	GC↑GGCCGC		I
*Nru*I		TCG↑CGA		ABCDEGIJKLMNOQRST
	*Bsp*68I	TCG↑CGA		F
*Nsp*I		RCATG↑Y		ABKM
	*Bst*NSI	RCATG↑Y		DI
*Nsp*BII		CMG↑CKG		A
	*Msp*A1I	CMG↑CKG		INR
*Pac*I		TTAAT↑TAA		NO
*Pfl*1108I		TCGTAG		
*Pfl*MI		CCANNNN↑NTGG		ANS
	*Acc*B7I	CCANNNN↑NTGG		IR
	*Esp*1396I	CCANNNN↑NTGG		F
	*Van*91I	CCANNNN↑NTGG		DFKM
*Ple*I		GAGTC(4/5)		N
	*Mly*I	GACTC(5/5)		
*Pma*CI		CAC↑GTG		AK
	*Bbr*PI	CAC↑GTG		MO
	*Eco*72I	CAC↑GTG		DEFR
	*Pml*I	CAC↑GTG		N
*Pme*I		GTTT↑AAAC		N
*Ppu*MI		RG↑GWCCY		ANO
	*Psp*5II	RG↑GWCCY		BDF
	*Psp*PPI	RG↑GWCCY		I
*Psh*AI		GACNN↑NNGTC		AKN
*Pst*I		CTGCA↑G	5(6)	ABCDEFGHIJKLMNOPQRST
*Pvu*I		CGAT↑CG		ABDEFGKLMNOPQRS
	*Bsp*CI	CGAT↑CG		E
	*Ple*19I	CGAT↑CG		I
*Pvu*II		CAG↑CTG	4(4)	ABCDEFGHIJKLMNOPQRST
*Rle*AI		CCCACA(12/9)		
*Rsa*I		GT↑AC		ABCDEFGIJLMNOPQRST
	*Afa*I	GT↑AC		K

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Table 1 cont.

Prototype	Isoschizomers	Recognition sequence[1]	Me site[2]	Commercial source[3]
	*Csp*6I	G↑TAC		DFN
*Rsr*II		CG↑GWCCG		BMNS
	*Cpo*I	CG↑GWCCG		ADFK
	*Csp*I	CG↑GWCCG		EOR
*Sac*I		GAGCT↑C	5(?)	ACEFGHJKLMNOPQRST
	*Ecl*136II	GAG↑CTC		DFN
	*Eco*ICRI	GAG↑CTC		R
	*Psp*124BI	GAGCT↑C		DI
	*Sst*I	GAGCT↑C		BCS
*Sac*II		CCGC↑GG		ACEGHJKLNOPQRST
	*Cfr*42I	CCGC↑GG		DF
	*Ksp*I	CCGC↑GG		M
	*Mlu*113I	CC↑GCGG		
	*Sfr*303I	CCGC↑GG		I
	*Sst*II	CCGC↑GG		BS
*Sal*I		G↑TCGAC	5(6)	ABCDEFGHIJKLMNOPQRST
*San*DI		GG↑GWCCC		E
*Sap*I		GCTCTTC(1/4)		N
*Sau*I		CC↑TNAGG		
	*Aoc*I	CC↑TNAGG		M
	*Axy*I	CC↑TNAGG		J
	*Bse*21I	CC↑TNAGG		I
	*Bsu*36I	CC↑TNAGG		ENRS
	*Cvn*I	CC↑TNAGG		B
	*Eco*81I	CC↑TNAGG		ADFKO
*Sca*I		AGT↑ACT		ABCDEFGJKLMNOPQRS
	*Acc*113I	AGT↑ACT		I
	*Eco*255I	AGT↑ACT		F
*Scr*FI		CC↑NGG	?(5)	DJMNOS
	*Bss*KI	↑CCNGG		N
	*Msp*R9I	CC↑NGG		I
*Sdu*I		GDGCH↑C		F
	*Bmy*I	GDGCH↑C		M
	*Bsp*1286I	GDGCH↑C		ADJKNR
*Sec*I		C↑CNNGG		
	*Bsa*JI	C↑CNNGG		N
	*Bse*DI	C↑CNNGG		DF
*Sex*AI		A↑CCWGGT		M
*Sfa*NI		GCATC(5/9)		IN
	*Bsc*AI	GCATC(4/6)		
*Sfe*I		C↑TRYAG		
	*Bfm*I	C↑TRYAG		F
	*Bst*SFI	C↑TRYAG		DI
	*Sfc*I	C↑TRYAG		N
*Sfi*I		GGCCNNNN↑NGGCC	?(4)	ABCDEGIJKLMNOPQRST
*Sgf*I		GCGAT↑CGC		R
*Sgr*AI		CR↑CCGGYG		M
*Sim*I		GGGTC(–3/0)		
*Sma*I		CCC↑GGG	2(4)	ABCDEFGHIJKLMNOPQRST

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Table 1 cont.

Prototype	Isoschizomers	Recognition sequence[1]	Me site[2]	Commercial source[3]
	*Cfr*9I	C↑CCGGG	2(4)	FO
	*Psp*AI	C↑CCGGG		E
	*Xma*I	C↑CCGGG	?(4)	ADINPRS
	*Xma*CI	C↑CCGGG		M
*Sml*I		C↑TYRAG		N
*Sna*I		GTATAC		
	*Bst*1107I	GTA↑TAC		DFKM
	*Bst*Z17I	GTA↑TAC		N
*Sna*BI		TAC↑GTA		ACEKLMNRS
	*Bst*SNI	TAC↑GTA		DI
	*Eco*105I	TAC↑GTA		FO
*Spe*I		A↑CTAGT		ABDEHJKLMNOPQRST
	*Acl*NI	A↑CTAGT		I
*Sph*I		GCATG↑C		ABCDEGHIJKLMNOPQRST
	*Bbu*I	GCATG↑C		R
	*Pae*I	GCATG↑C		F
*Spl*I		C↑GTACG		AK
	*Bsi*WI	C↑GTACG		MNO
	*Pfl*23II	C↑GTACG		DF
	*Psp*LI	C↑GTACG		I
	*Sun*I	C↑GTACG		B
*Srf*I		GCCC↑GGGC		EO
*Sse*8387I		CCTGCA↑GG		AK
	*Sbf*I	CCTGCA↑GG		DI
	*Sda*I	CCTGCA↑GG		F
*Sse*8647I		AG↑GWCCT		
*Ssp*I		AAT↑ATT	?(6)	ABCDEFIJKLMNOQR
*Stu*I		AGG↑CCT		ABEJKLMNPQRST
	*Aat*I	AGG↑CCT		O
	*Eco*147I	AGG↑CCT		DF
	*Pme*55I	AGG↑CCT		I
	*Sse*BI	AGG↑CCT		C
*Sty*I		C↑CWWGG		BCEJMNRS
	*Bss*T1I	C↑CWWGG		I
	*Eco*130I	C↑CWWGG		DF
	*Eco*T14I	C↑CWWGG		AK
	*Erh*I	C↑CWWGG		I
	*Swa*I	ATTT↑AAAT		M
	*Sml*I	ATTT↑AAAT		DI
*Taq*I		T↑CGA	4(6)	ABCDEFGJLMNOPQRST
	*Tth*HB8I	T↑CGA	4(6)	AK
*Taq*II[8]		CACCCA(11/9)		
*Taq*II[8]		GACCGA(11/9)		
*Tat*I		WGTACW		
*Tau*I		GCSGC		
*Tfi*I		G↑AWTC		N
*Tse*I		G↑CWGC		N
*Tsp*45I		↑GTSAC		N
*Tsp*4CI		ACN↑GT		

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Table 1 cont.

Prototype	Isoschizomers	Recognition sequence[1]	Me site[2]	Commercial source[3]
*Tsp*EI		↑AATT		LO
	*Sse*9I	↑AATT	2(6)	DI
	*Tsp*509I	↑AATT		N
*Tsp*RI		CAGTG(2/–7)		N
*Tth*111I		GACN↑NNGTC		ADIKNQR
	*Asp*I	GACN↑NNGTC		M
	*Pfl*FI	GACNNNGTC		N
*Tth*111II		CAARCA(11/9)		
*Uba*DI		GAACNNNNNNTCC		
*Uba*EI		CACCTGC		
*Vsp*I		AT↑TAAT	5(6)	BDEFIR
	*Ase*I	AT↑TAAT		AJNO
	*Asn*I	AT↑TAAT		MS
	*Psh*BI	AT↑TAAT		K
*Xba*I		T↑CTAGA	6(6)	ABCDEFGHIJKLMNOPQRST
*Xcm*I		CCANNNNNN↑NNNNTGG		AN
*Xho*I		C↑TCGAG		ABCDEFGHJKLMNOPQRST
	*Pae*R7I	C↑TCGAG	5(6)	N
	*Sci*I	CTC↑GAG		
	*Sfr*274I	C↑TCGAG		I
*Xho*II		R↑GATCY		EMR
	*Bst*X2I	R↑GATCY		DI
	*Bst*YI	R↑GATCY		BN
	*Mfl*I	R↑GATCY		AK
*Xma*III		C↑GGCCG	4(5)	BE
	*Bst*ZI	C↑GGCCG		R
	*Eag*I	C↑GGCCG	?(5)	NPS
	*Ecl*XI	C↑GGCCG		M
	*Eco*52I	C↑GGCCG		ADFKOR
*Xmn*I		GAANN↑NNTTC		DENR
	*Asp*700I	GAANN↑NNTTC		M
	*Mro*XI	GAANN↑NNTTC		I

1. Recognition sequences use the standard abbreviations (*European Journal of Biochemistry* 150, 1–5 (1985)) to represent ambiguity.

R = A or G	B = not A (C or G or T)
Y = C or T	D = not C (A or G or T)
M = A or C	H = not G (A or C or T)
K = G or T	V = not T (A or C or G)
S = G or C	N = A or C or G or T
W = A or T	

Recognition sequences are written from 5′ to 3′, only one strand being given, and the point of cleavage is indicated by an arrow (↑). When no arrow appears, the precise cleavage site has not been determined. For enzymes such as *Bci*VI, which cleaves away from its recognition sequence, the sites of cleavage are indicated in parentheses. Thus GTATCC (6/5) indicates cleavage as shown below:

5′-GTATCCNNNNNN↑-3′
3′-CATAGGNNNNN↑-5′

In all cases the recognition sequences are oriented so that the cleavage sites lie on their 3′-side.

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2. The site of methylation by the cognate methylase when known is indicated as follows. The first number shows the base within the recognition sequence that is modified. A negative number indicates the complementary strand, numbered from the 5′ base of that strand. The number in parentheses indicates the specific methylation involved. (6) = N^6-methyladenosine; (5) = 5-methylcytosine; (4) = N^4-methylcytosine. Thus for *Alw*26I the designation 3(5), –4(6) signifies the following pattern of methylation:

	1	2	3	4	5	
5′	G	T	5mC	T	C	3′
3′	C	6mA	G	A	G	5′
	–1	–2	–3	–4	–5	

3. Commercial sources of restriction enzymes are abbreviated as follows:

   A, Amersham Life Sciences-USB (10/96); B, Life Technologies Inc., Gibco-BRL (10/96); C, Minotech Molecular Biology Products (10/96); D, Angewandte Gentechnologie Systeme (10/96); E, Stratagene (10/96); F, Fermentas MBI (10/96); G, Appligène Oncor (10/96); H, American Allied Biochemical, Inc. (10/96); I, *Sib* Enzyme Ltd (10/96); J, Nippon Gene Co., Ltd (10/96); K, Takara Shuzo Co. Ltd (10/96); L, NBL Gene Sciences Ltd (10/96); M, Boehringer-Mannheim (11/96); N, New England BioLabs (11/96); O, Toyobo Biochemicals (10/96); P, Pharmacia Biotech Inc. (10/96); Q, CHIMERx (5/96); R, Promega Corporation (10/96); S, Sigma (10/96); T, Advanced Biotechnologies Ltd (10/96). The date in parentheses indicates the most recent update.

4. Enzymes that cut on both sides of their recognition sequence, such as *Bae*I, *Bcg*I, *Bsp*24I, *Cje*I and *Cje*PI, have 4 cleavage sites each instead of 2. For example, *Bsp*24I cleaves as indicated:

   5′ ↑NNNNNNNNGACNNNNNNTGGNNNNNNNNNNNN↑ 3′
   3′ ↑NNNNNNNNNNNNNCTGNNNNNNACCNNNNNNN↑ 5′

   This is described in Table 2 and some REBASE reports as *Bsp*24I (8/13)GACNNNNNNTGG(12/7). Thus the recognition site is excised in a fragment, 32 base pairs long, with 5-base 3′-extensions at each end.

5. *Dpn*I requires the presence of 6-methyladenosine within the recognition sequence GmATC.

6. *Eco*RII isoschizomers fall into two classes based upon their sensitivity to methylation. *Eco*RII will not cleave when the second cytosine in the recognition sequence is methylated to 5-methylcytosine whereas *Mva*I will cleave such a sequence. Isoschizomers of *Eco*RII that are like *Mva*I are indicated by +.

7. *Mbo*I isoschizomers fall into two classes based upon their sensitivity to methylation. *Mbo*I will not cleave when the recognition sequence contains 6-methyladenosine whereas *Sau*3AI will not cleave when its recognition sequence contains 5-methylcytosine. Isoschizomers of *Mbo*I that are like *Sau*3AI are indicated by +.

8. *Taq*II differs from other restriction enzymes in recognizing two distinct sequences: GACCG and CACCCA.

Table 2. Type I enzymes

Prototype enzyme	Recognition sequence[1]	Me site[2]
*Cfr*AI	GCANNNNNNNNGTGG	
*Eco*AI	GAGNNNNNNNGTCA	2(6),–3(6)
*Eco*BI	TGANNNNNNNNTGCT	3(6),–4(6)
*Eco*DI	TTANNNNNNNGTCY	
*Eco*DR2	TCANNNNNNGTCG	
*Eco*DR3	TCANNNNNNNATCG	
*Eco*DXXI	TCANNNNNNNRTTC	
*Eco*EI	GAGNNNNNNNATGC	
*Eco*KI	AACNNNNNNGTGC	2(6),–3(6)
*Eco*R124I	GAANNNNNNRTCG	3(6),–3(6)
*Eco*R124II	GAANNNNNNNRTCG	–3(6)
*Eco*RD2	GAANNNNNNRTTC	
*Eco*RD3	GAANNNNNNNRTTC	
*Eco*prrI	CCANNNNNNNRTGC	
*Sty*LTIII	GAGNNNNNNRTAYG	2(6),–4(6)
*Sty*SJ	GAGNNNNNNGTRC	
*Sty*SPI	AACNNNNNNGTRC	2(6),–3(6)
*Sty*SQ	AACNNNNNNRTAYG	

For notes and abbreviations see Table 1

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Appendix F

Table 3. Type III enzymes

Prototype enzyme	Recognition sequence[1]	Me site[2]
*Eco*PI	AGACC	3(6)
*Eco*P15I	CAGCAG(25/27)	5(6)
*Hin*fIII	CGAAT	
*Sty*LTI	CAGAG	4(6)

For notes and abbreviations see Table 1

Table 4. Homing endonucleases

Enzyme	Sequence around one cleavage site[1]	Commercial source[2]
Endo.*Sce*I	GATGCTGT_AGGC↑ATAGGCTTGGTT	
HO-endo	CTTTCCGC_AACA↑GTATAATT	
I-*Ceu*I	TCTAACTATAACGGTC_CTAA↑GGTAGCGAG	N
I-*Chu*I	GAAGGTTTGGCAC_CTCG↑ATGTCGGCTCATC	
I-*Cpa*I	CGATCCTAAGGTAG_CGAA↑ATTCA	
I-*Cpa*II	TCCGGCTA_ACTC↑TGTGCCAG	
I-*Cre*I	CTGGGTTCAAAACGTC_GTGA↑GACAGTTTGG	
I-*Csm*I	GTACTAGCATGGGGTCAAATGTCTTTCTGG	
I-*Dmo*I	ATGCCTTGCCGG_GTAA↑GTTCCGGCGCGCAT	
I-*Por*I	GCGAGCCCGTAA_GGGT↑GTGTACGGG	
I-*Ppo*I	CTATGACTCTC_TTAA↑GGTAGCCAAAA	NR
I-*Sca*I	TGTCACATTGAGGTGCACTAGTTATTAC	
I-*Sce*I	TTACGCTAGGG_ATAA↑CAGGGTAATA	M
I-*Sce*II	TTCTGATTCTTTGGTC_ACCC↑TGAAGTATAT	
I-*Sce*III	CTTGGAGGTTTTGG_TAAC↑TATTTATTACCA	
I-*Sce*IV	AATTTTCTCATG_ATTA↑GCTCTAATCCATGG	
I-*Tev*I	AGTGGTATCA_AC↑GCTCAGTAGATG	
I-*Tev*II	GCTTATGAGTATGAAGTGAACAC_GT↑TATTC	
I-*Tev*III	↑TA_TGTATCTTTTGCGTGTACCTTTAACTTC	
PI-*Psp*I	AAAATCCTGGCAAACAGCTA_TTAT↑GGGTAT	N
PI-*Sce*I	ATCTATGTCGG_GTGC↑GGAGAAAGAGGTAAT	N
PI-*Tli*I	TCTTTATGCGG_ACAC↑TGACGGCTTTTAT	N
PI-*Tli*II	AAATTGCTTGCAAACAGCTATTACGGCTAT	

1. The cleavage sites, where known, are indicated by ↑ on the strand presented and by _ on the complementary strand.

2. The commercial sources are M: Boehringer-Mannheim (11/96); N: New England BioLabs (11/96); R: Promega Corporation (10/96).

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Appendix G

Sequence-rule priorities of some common ligands in molecular entities

The names of some common ligands are listed alphabetically below, the numbers preceding them indicating the relative priorities assigned to the ligands under the **sequence rule**. A higher number denotes greater preference; for example, a hydroxy group (numbered 57) takes precedence over an amino group (numbered 43). It should be noted that any change to the structure of a listed ligand may alter the order of preference. Where a ligand consists of or contains a heavy or radioactive isotope of hydrogen, the relative priorities are tritium > deuterium > protium. Racemates with a single chiral centre are labelled (*RS*); extensions of the sequence rule are used in the *E*/*Z*, *pro-R*/*pro-S*, *pro-E*/*pro-Z*, and *Re*/*Si* nomenclature systems.

64 acetoxy
36 acetyl
48 acetylamino
21 acetylenyl
10 allyl
43 amino
44 ammonio ($^{+}H_3N$–)
37 benzoyl
49 benzoylamino
65 benzoyloxy
13 benzyl
60 benzyloxy
41 benzyloxycarbonyl
50 benzyloxycarbonylamino
75 bromo
42 *tert*-butoxycarbonyl
5 butyl
16 *sec*-butyl
19 *tert*-butyl
38 carboxy
74 chloro
17 cyclohexyl
52 diethylamino
51 dimethylamino
34 2,4-dinitrophenyl
28 3,5-dinitrophenyl
59 ethoxy
40 ethoxycarbonyl
3 ethyl
46 ethylamino
68 fluoro
35 formyl
63 formyloxy
62 glycosyloxy
7 hexyl
1 hydrogen
57 hydroxy
76 iodo
9 isobutyl
8 isopentyl
20 isopropenyl
14 isopropyl
69 mercapto (HS–)
58 methoxy
39 methoxycarbonyl
2 methyl
45 methylamino
71 methylsulfinyl
66 methylsulfinyloxy
72 methylsulfonyl
67 methylsulfonyloxy
70 methylthio (CH_3S–)
11 neopentyl
56 nitro
27 *m*-nitrophenyl
33 *o*-nitrophenyl
24 *p*-nitrophenyl
55 nitroso
6 pentyl
61 phenoxy
22 phenyl
47 phenylamino
54 phenylazo
18 propenyl
4 propyl
29 1-propynyl
12 2-propynyl
73 sulfo (HO_3S–)
25 *m*-tolyl
30 *o*-tolyl
23 *p*-tolyl
53 trimethylammonio
32 trityl
15 vinyl
31 2,6-xylyl
26 3,5-xylyl

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Appendix H
Species names

Below is a list of genera/species cited frequently in this Dictionary, together with their common names, where applicable. The asterisked names have their own entries in the Dictionary.

**Agrobacterium*
Amanita a genus of toadstools; *A. muscaria* is fly agaric,
A. phalloides the 'death-cap' (deadly agaric)
**Arabidopsis thaliana*
**Aspergillus*
**Bacillus*
Bos taurus cattle
Brassica a genus of cruciferous plants; *B. napus* is the swede, *B. oleracea* includes the cabbage, cauliflower, etc.
Caenorhabditis elegans a nematode
Candida a genus of yeasts
Canis familiaris the dog
Chlamydomonas reinhardtii a unicellular green alga
**Clostridium*
Corynebacterium a genus of **coryneform** (def. 2) bacteria
**Dictyostelium discoideum*
Digitalis the foxglove genus
**Drosophila*
**Escherichia coli*
Euglena a unicellular, flagellate alga belonging to the Euglenophyta
Gallus gallus the domestic fowl
Haemophilus influenzae an aerobic, nonmotile Gram-negative rod
Halobacterium halobium a halophilic archaebacterium
Klebsiella a genus of Gram-negative rod nonmotile bacteria
Lactobacillus a genus of **lactic-acid bacteria**
Lycopersicon esculentum the tomato
Mus musculus the mouse
**Mycobacterium*
**Neurospora*
Nocardia a genus of rod or filamentous Gram-positive nonmotile bacteria
**Paramecium*
Penicillium mould
Pisum sativum the garden pea
**Plasmodium*
Pseudomonas a genus of Gram-negative rod-shaped motile bacteria
Rattus norvegicus the rat
**Rhizobium*
**Saccharomyces*
**Salmonella*
**Schizosaccharomyces pombe*
Shigella a genus of nonmotile Gram-negative rod **coliform** bacteria
**Staphylococcus*
**Streptococcus*
**Streptomyces*
Sus scrofa the pig
**Tetrahymena*
Thermus aquaticus a thermophilic archaebacterium
Trypanosoma a genus of parasitic protozoans; *see* **trypanosome**
**Xenopus laevis*
Zea mays maize (corn)

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